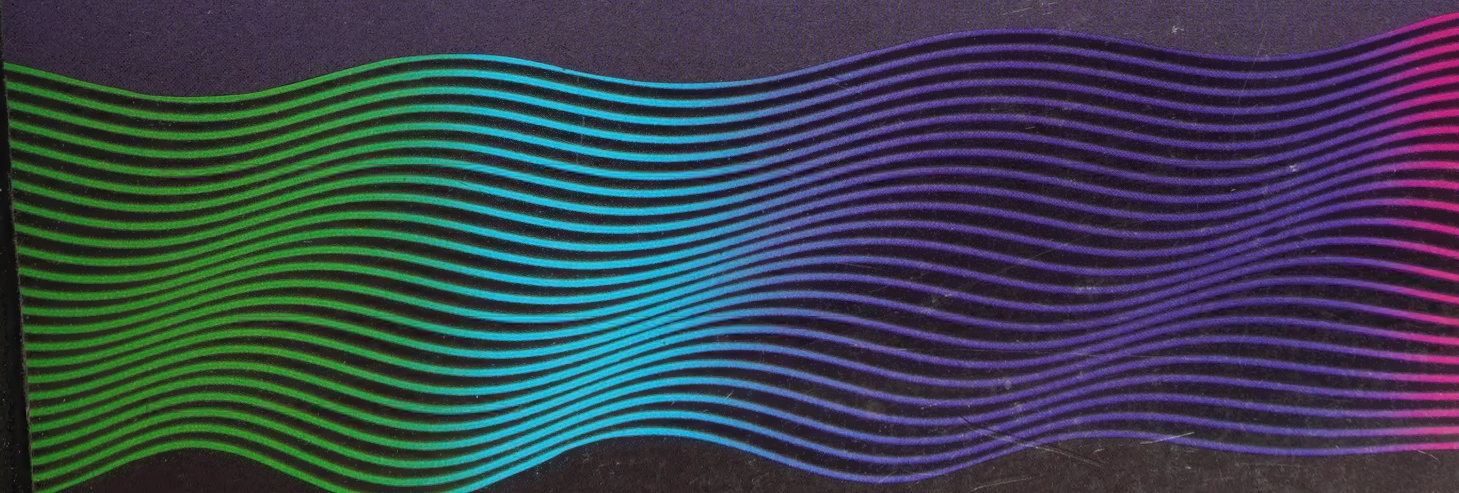




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Moulting and Mating of Snow Crabs, *Chionoecetes opilio* (O. Fabricius), in Shallow Waters of the Northwestern Gulf of Saint Lawrence

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Sainte-Marie, B., and F. Hazel. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. *Can. J. Fish. Aquat. Sci.* 49: 1282–1293.

Chionoecetes opilio in baie Sainte-Marguerite, Gulf of Saint Lawrence, were sampled by beam trawl in spring from 1988 to 1991 and by divers in March 1991 to document an hypothesized annual moult in shallow waters. Each spring, *C. opilio* occurred at 4–20 m of depth where 29.3–97.3% of males and 20.3–81.4% of females were moulting or recently moulted. Males and females ≥ 25 mm carapace width (CW) moulted only on bottoms < 60 m. Females were mature at ≥ 39.6 mm CW and males were morphometrically mature at ≥ 40.4 mm CW. Overall, 0.3% of morphometrically mature ($N = 575$) and 23% of morphometrically immature ($N = 826$) males ≥ 40 mm CW, exclusive of soft-shelled, had a visible second carapace. These and other data support the hypothesis of a terminal moult coincident with morphometric maturity. Pubescent females mated with males 59.9–109.3 mm CW (88% were < 95 mm CW), 97% of which were morphometrically mature ($N = 120$). Mean size of these males was greater than that of males grasping immature females or other males, indicating male competition for pubescent females. Morphometrically mature males were larger on bottoms > 80 m deep, where multiparous females concentrated, than on shallower bottoms.

La population de *Chionoecetes opilio* de la baie Sainte-Marguerite, dans le golfe Saint-Laurent, a été échantillonnée à l'aide d'un chalut à perche au printemps de 1988 à 1991 et par des plongeurs en mars 1991, afin de vérifier l'hypothèse d'une mue annuelle en eaux peu profondes. Chaque printemps, l'espèce était présente sur des fonds profonds de 4 à 20 m où 29,3–97,3 % des mâles et 20,3–81,4 % des femelles étaient en mue ou avaient récemment mué. Les mâles et les femelles ≥ 25 mm de largeur de carapace (Lc) mueaient seulement sur des fonds < 60 m de profondeur. La maturité des femelles survenait à $\geq 39,6$ mm Lc et les mâles atteignaient la maturité morphométrique à $\geq 40,4$ mm Lc. Dans l'ensemble, 0,3 % des mâles morphométriquement matures ($N = 575$) et 23 % des mâles morphométriquement immatures ($N = 826$) ≥ 40 mm Lc, excluant les récemment mués, avaient une deuxième carapace visible. Ces données, ainsi que d'autres, appuient l'hypothèse d'une mue terminale qui coïncide avec la maturité morphométrique. Les femelles pubères s'accouplaient avec des mâles de 59,9 à 109,3 mm Lc (88 % avaient < 95 mm Lc) parmi lesquels 97 % étaient morphométriquement matures ($N = 120$). La taille moyenne de ces mâles était supérieure à celle des mâles accouplés avec des femelles immatures ou avec d'autres mâles, ce qui indique qu'il y a compétition entre mâles pour les femelles pubères. Les mâles morphométriquement matures sur les fonds > 80 m de profondeur, où se concentraient les femelles multipares, étaient plus grands que ceux en plus faible profondeur.

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The snow crab *Chionoecetes opilio* (O. Fabricius) is an economically important majid in the Northwest Atlantic and North Pacific (Bailey and Elner 1989). On the eastern coast of Canada, the fishery is conducted with baited traps and is regulated by a minimum size of 95 mm carapace width (CW). Only males are harvested because females do not exceed 95 mm CW. Not all males are equally trapable; catches often are strongly biased in favour of large-clawed, so-called morphometrically mature males (Conan 1986; E. G. Dawe and J. M. Hoenig, Department of Fisheries and Oceans, Newfoundland, pers. comm.; B. Sainte-Marie, unpubl. data). The morphometrically mature condition is reportedly reached at ≥ 52 mm CW (Conan and Comeau 1986).

The moulting and reproduction of *C. opilio* are poorly documented and subjects of controversy. These events are interdependent, as females mate for the first time in a soft-shell condition, while soft-shelled males are unable to mate (Conan et al. 1990). It has been proposed that males have a terminal

moult, so that growth is determinate (Powles 1968; Miller and O'Keefe 1981), as appears to be the rule in majids (Hartnoll 1963). At the moult to morphometric maturity, there occurs a change in the allometry of chelae which determines two male morphs: morphometrically immature or small-clawed and morphometrically mature or large-clawed. Recently, this moult was hypothesized to be the terminal moult (O'Halloran 1985; Conan and Comeau 1986). However, Dawe et al. (1991) refuted evidence in support of this hypothesis and challenged it on the basis of inferential and statistical arguments, and of some disparate field and laboratory observations. The proposed alternative is that moulting and growth continue, but at a much reduced tempo (Donaldson and Johnson 1988; Dawe et al. 1991). For females, the moult to sexual maturity is widely recognized as a terminal moult (e.g. Yoshida 1941; Ito and Kobayashi 1967; Watson 1972; Conan et al. 1990), although Hooper (1986) stated the contrary but with no quantitative data in support.

Conan and Comeau (1986) also concluded that only morphometrically mature males ≥ 95 mm CW mate with multiparous females. But Comeau (1987) documented gonadic maturity in some morphometrically immature males, and Ennis et al. (1988, 1990) observed that males as small as 62 mm CW, a minority of which were morphometrically immature, engaged in precopulatory embrace with multiparous females. Whether this was followed by the production of a viable brood or whether these small males in effect fertilized eggs in an eventual brood is uncertain (Elner and Beninger 1989). Mating of pubescent females (i.e. females committed to moult, with immature external features but ripe gonads), which presumably occurs earlier in the year than that of multiparous females, has not been observed in the field (Conan et al. 1990). Nevertheless, Conan and Comeau (1986) stated that mating of pubescent females with morphometrically mature males < 95 mm CW "is likely to be a rare event" in nature. Yet, laboratory observations (Watson 1970; Conan et al. 1990) suggest that the mating of pubescent females is noncompetitive: both morphometrically mature and morphometrically immature males (with functional gonads) mate with pubescent females, and size dimorphism in favour of males is not a strict prerequisite for mating.

The terminal moult hypothesis and the reproductive competency of different size or maturity classes of males are critical issues, and their resolution has profound implications for management practices. If a terminal moult exists, a substantial fraction of males never reach a commercial size, and thus the minimum legal size does not maximize yield per recruit (Conan and Comeau 1986). Moreover, predictions of year-class strength at recruitment by the direct assessment of prerecruits (Jamieson 1986) would have to take into account the fact that a fraction of the male population will never reach a commercial size. Also, mortality could be calculated for morphometrically mature males by determining age structure of exoskeletons using shell condition indices or radioisotope ageing techniques. Finally, if male size at morphometric maturity is genetically determined, and only morphometrically mature males effectively mate, fishery selection against large males could lead to male dwarfism (Conan 1986; Elner et al. 1986; Bailey and Elner 1989).

Most field studies of *C. opilio* in the Northwest Atlantic have been limited to late spring, summer, and early fall, and rare winter and early spring data were derived from selective trap samples (e.g. Miller and O'Keefe 1981). Ice has so far prevented trawl sampling in late winter and early spring when, presumably, females and males moult and pubescent females mate (Conan et al. 1990). Also, direct observation by SCUBA diving is generally impossible because of the great depths at which *C. opilio* is distributed. Most knowledge of reproductive biology and moulting of *C. opilio* thus comes from laboratory observations, or is derived from field studies of a small, apparently isolated and unexploited population in Bonne Bay (Newfoundland). There, some sexually paired males move to shallow waters in the spring, in the course of a spring breeding migration (Taylor et al. 1985; Hooper 1986), or because they are excluded from deeper areas by more competitive males (Comeau et al. 1991). There is only one other published report of large numbers of *C. opilio* in shallow waters: baie Sainte-Marguerite, on the north shore of the Gulf of Saint Lawrence, was the site of a mass beaching of snow crabs in the late winter of 1988 (Sainte-Marie et al. 1988). Stranded snow crabs were moulting or had clean soft shells, and most were small males (< 75 mm CW). The combined effects of low spring tides, storms, and exceptionally cold temperatures probably were re-

sponsible for the beaching. It was hypothesized that snow crabs had moved onto the infralittoral grounds from offshore areas, although the reasons for this supposed annual event were unclear. The baie Sainte-Marguerite snow crab population belongs to a commercially exploited stock (Middle North Shore area, Dufour and Coutu 1990).

Field work was conducted in baie Sainte-Marguerite in the early spring from 1988 to 1991 to determine if snow crabs occurred and moulted annually on the infralittoral grounds. We show that they did, and we report on previously undocumented aspects of the biology of *C. opilio* related to moulting and reproduction. We were able to determine the relative frequency of moulting of morphometrically immature and morphometrically mature males, and observed for the first time the mating of pubescent females in nature.

Materials and Methods

Study Site and Sampling

Baie Sainte-Marguerite is located on the north shore of the Gulf of Saint Lawrence (Fig. 1). In early spring, throughout the northern Gulf of Saint Lawrence, ice is a major factor that limits the scope of work and the type and availability of ships. Shifting ice and frequent gales make any kind of sampling arduous and risky and, as a consequence, the timing, number, and consistency of our observations varied from year to year.

On 30 March 1988, 25 March 1989, 25–30 April 1990, and 10–15 April 1991, baie Sainte-Marguerite was sampled with a beam trawl with a 2.5-m effective fishing width and 25-mm stretched mesh size. In 1988, ≈ 8750 m² of bottom was sampled in one tow (Sainte-Marie et al. 1988); in other years, tows lasted 15–25 min of bottom time at 2.5 knots, so ≈ 2896 to ≈ 4826 m² of bottom was sampled by tow. In 1988 and 1989, we sampled only the shallow (4 to ≤ 20 m) northwest part of the bay, where snow crabs were stranded in 1988 (Sainte-Marie et al. 1988). In 1990 and 1991, samples came from randomly allocated positions in each of three depth strata, 4 to ≤ 20 m (shallow), > 20 to ≤ 80 m (intermediate), and > 80 to 140 m (deep), within the study area shown in Fig. 1 (inset). Below the 140-m isobath the population of *C. opilio* is exceedingly sparse (B. Sainte-Marie, unpubl. data); we are thus confident that our sampling in 1990 and 1991 was representative of the whole *C. opilio* population.

Trawl contents were sorted on board, and snow crabs or their remains were immediately enumerated according to the following categories: exuviae (i.e. cast shells) and live individuals with a visible second shell, a clean shell, or a dull or dirty shell. Exuviae were either complete (i.e. carapace, appendages, and abdomen were attached) or incomplete (i.e. carapace separated from cephalothoracic sternites and abdomen, most appendages lacking, exuviae parts severely eroded and damaged). The number of incomplete exuviae was tentatively determined from counts of complete carapaces and of cephalothoracic sternites. However, the derived numbers should be considered with caution because the two counts were not the same and because broken carapaces and cephalothoracic sternites were abundant. Individuals with a visible second shell were characterized by detachment of the old shell that was raised in posterior regions of the body so that a new, soft carapace was more or less exposed. This condition can be detected up to 3 wk before ecdysis by careful examination of the posterior margin of the carapace (Watson 1971). Clean shells were iridescent, had no wear or epizoites, and were either soft (chela buckle or shatter when pressed with thumb) or hard.

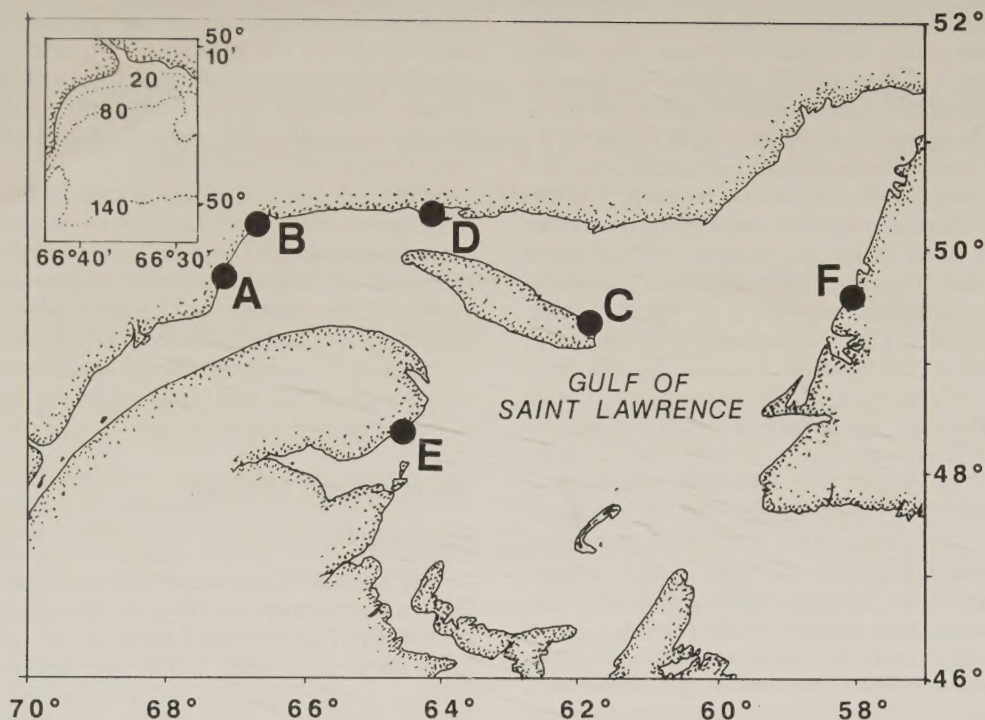


FIG. 1. Map of the Gulf of Saint Lawrence showing baie Sainte-Marguerite (B and inset, which represents the study area). Sites of documented beachings of *C. opilio* are baie Sainte-Marguerite (B), Pointe-aux-Anglais (A), and Fox Bay, Anticosti (C). Sites of documented shallow-water (<35 m) occurrence of *C. opilio* are baie Sainte-Marguerite (B), Mingan Archipelago (D), Port-Daniel in baie des Chaleurs (E), and Bonne Bay (F).

Dull or dirty shells (here collectively called dirty) were only faintly or not at all iridescent and were scarred, worn, and often colonized by epizoids.

All live individuals and complete exuviae were sexed. We attempted to sex incomplete exuviae by examination of the abdomens or of the imprint of abdomens on cephalothoracic sternites: the male abdomen is triangular in shape, while the female abdomen is more rectangular in immature specimens and is a large rounded shield in mature specimens (see also below).

Live females and female exuviae were classified as immature (flat abdomen, narrower than cephalothoracic sternites) or mature (rounded abdomen, almost as broad as cephalothoracic sternites) by visual inspection. Carapace width was determined with a vernier caliper. Mature females were further divided into primiparous (first brood) and multiparous (second or later broods) based on exoskeleton condition: the former had clean shells and did not have mating scars, while multiparous females had dirty shells and pereopods barred with distinct mating scars (Somerton and Meyers 1983; Paul 1984). It should be noted, however, that the use of mating scars alone to determine the reproductive status of females has been faulted (Elnor and Beninger 1989; see Donaldson and Adams 1989 for evidence of matings without injury in *C. bairdi*, in agreement with our own unpublished observations on *C. opilio*).

For all live males and complete male exuviae, carapace width and right chela height (CH) were measured with a vernier caliper to the nearest 1 mm in 1988 and to the nearest 0.1 mm in 1989, 1990, and 1991. Chela height was measured between spines, at the highest point of the propodus. We used this measure and the vernier caliper, rather than the height of propodus inclusive of spines and the modified caliper

commonly used by other workers (Watson and Wells 1970), because measurement variability resulting from spine erosion during intermoult was reduced. Male exuviae in one very large sample were enumerated, but for lack of time, morphometric measurements were performed only on a subsample.

Following Conan and Comeau (1986), principal component analysis was used for the a priori classification of a sample of 88 males (40–110 mm CW), taken in 1989, as morphometrically immature or morphometrically mature, using carapace width and chela height, length, and width (B. Sainte-Marie, unpubl. data). Discriminant analysis was then used on these males (Conan and Comeau 1986) to produce a separating line based on chela height and carapace width:

$$\ln(\text{CH}) = 1.2209 \ln(\text{CW}) - 2.6077.$$

This discriminant function was used to score unclassified males as morphometrically immature or morphometrically mature; the probability of misclassifying a given individual was 0.9%. Although Dawe et al. (1991) have argued convincingly that the cutting line obtained by this method is no more objective than one fitted by eye, the reader will be satisfied that the calculated line effectively separates two clouds of points in Fig. 2B.

To further assess the number of males that were committed to moult in both categories of morphometric maturity, we examined two samples of males collected by trawl from the three depth strata of baie Sainte-Marguerite in April 1991. Each sample comprised individuals selected to be clearly morphometrically immature or morphometrically mature (i.e. that lay either well above or well below the cutting line in Fig. 2B) and distributed almost evenly among 20-mm size classes ranging from ≥ 40 to 120 mm CW. For the first sample, we simply dissected individuals to determine the presence of an underlying carapace. For the second sample, we determined

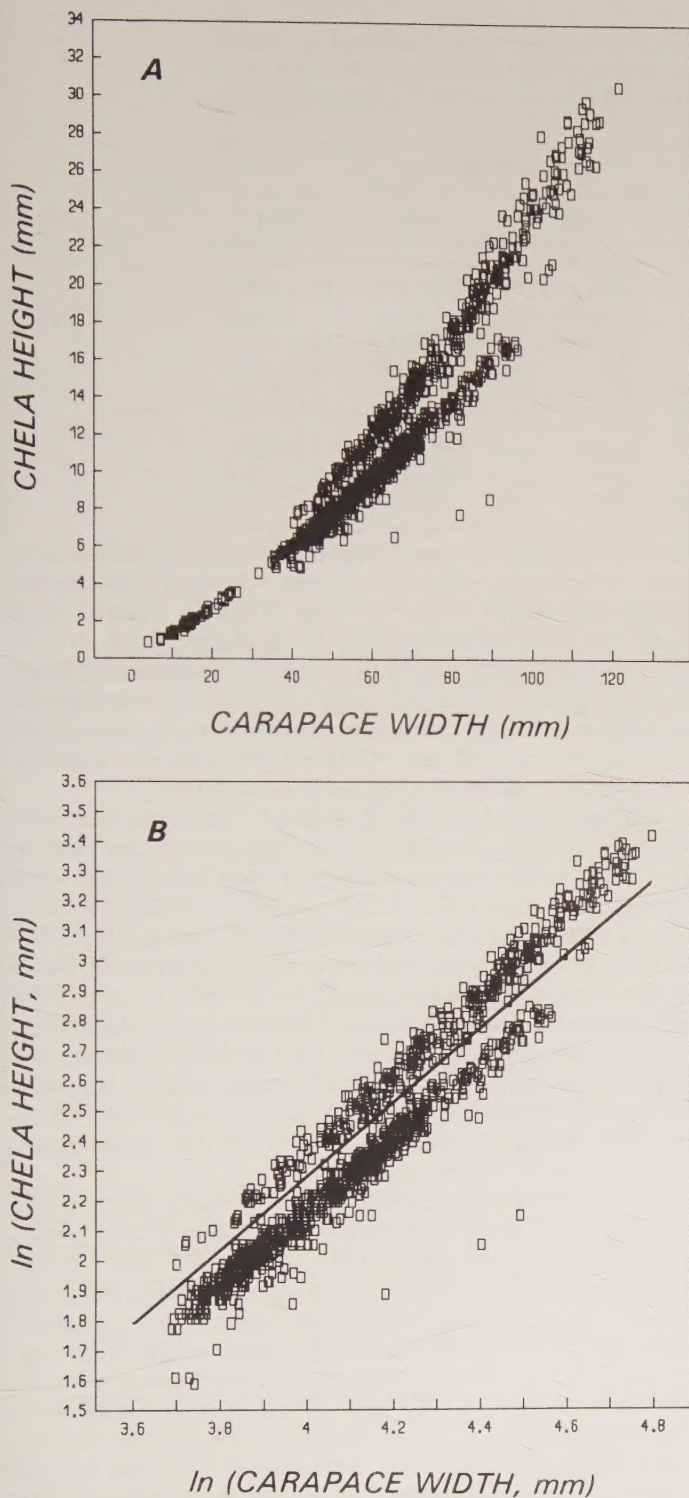


FIG. 2. Plot of right chela height on carapace width for male *C. opilio* collected by beam trawl in baie Sainte-Marguerite in April 1990. (A) Untransformed data for all males; (B) natural logarithms of data for males ≥ 40 mm CW with cutting line determined by discriminant analysis. Note the presence of very small morphometrically mature males and of several males with a diminutive right chela.

moult stages by examination of mouth parts (Moriyasu and Mallet 1986). All males in D_0 or later stages (D_1 – D_4) were considered to be committed to moult.

On 20–27 March 1991, we used SCUBA diving in baie Sainte-Marguerite to collect all sexually paired snow crabs along two transects perpendicular to the shore and separated by

1.8 km. Bottoms from 4 to 35 m depth were explored, and all couples in pre- and postcopulatory embrace (rostrum to rostrum, one individual holding the other) and in copulatory embrace (sternum to sternum) were collected. Depth of occurrence was recorded, and pairs were isolated in individual dive bags that were floated to the surface where we determined sex, carapace width and condition, and right chela height for males or width of the fifth abdominal sternite for females. The state of gonads of sexually paired females was determined initially by dissection, and then more simply by visual inspection. Indeed, when gonads were ripe (large, bright orange ovaries), they showed through the exoskeleton at the suture between cephalothorax and abdomen, and through the first few abdominal tergites or sternites. As a precautionary measure, all females with a visible second shell and inconspicuous gonads, called immature sterile hereafter, were dissected to verify the immature state of gonads. Immature females that had a visible second shell and ripe gonads were committed to becoming mature, as confirmed by field and laboratory observations (see below; B. Sainte-Marie, unpubl. data) and are thus called pubescent.

Additionally, on 26 March 1991, SCUBA divers collected three pubescent females and one male with a visible second shell, and they were transferred to a 200-L shipboard holding tank. These individuals moulted some time during the night and were measured early the following morning. Carapace width and width of the fifth abdominal sternite (females) or height of the right chela (males) were measured on exuviae and postmoulted individuals.

Data Analysis

Simple statistics (mean and standard deviation, median and range) were used to describe data. When data were normally distributed and were homoscedastic, as determined respectively by the Kolmogorov–Smirnov test and Bartlett's test, the *t*-test was used to compare mean values of two samples (Sokal and Rohlf 1981). For the comparison of several samples that did not meet conditions of normality and homoscedasticity, we used the Kruskal–Wallis analysis of variance by ranks in conjunction with Dunn's multiple comparison test (Daniel 1978). A simple (Pearson) correlation was used to check for effects of depth on the size distribution of sexually paired males and to determine if there was any relation between female and male body size in sexually paired couples. A two-way test of independence (*G*-test with William's correction, Sokal and Rohlf 1981) was used to test the hypothesis that the estimated frequency of moulting morphometrically immature males, relative to total population of morphometrically immature males, was independent of the method used to assess readiness to moult.

Results

Size of Live Snow Crabs and Exuviae

The range of carapace widths for exuviae and live *C. opilio* collected by trawl appears in Table 1. Very small (<15 mm CW) *C. opilio* were apparently absent from the shallow depth stratum, but this may be an artifact of sampling. Because trawl mesh size was 25 mm, we restrict further analyses and discussion to live individuals or exuviae ≥ 25 mm CW; mean density estimates for these snow crabs are shown in Table 2.

Snow crabs in baie Sainte-Marguerite may reach morphometric maturity (males) or sexual maturity (females) at

TABLE 1. Range of carapace widths of live *C. opilio* and of complete exuviae collected by trawl in three depth strata of baie Sainte-Marguerite in March 1988 and 1989 and in April 1990 and 1991. Individuals as small as 2.8 mm CW were collected from >20 to ≤80 and >80 to 140 m strata, but sex determination was unreliable when CW < 5 mm.

Depth stratum (m)	Sex	Condition	Carapace width (mm)			
			1988	1989	1990	1991
4 to ≤20	Female	Exuviae	—	28.6–41.7	—	—
		Live	28–60	36.6–56.4	15.1–53.9	15.0–68.9
	Male	Exuviae	—	21.3–70.9	34.7–93.3	—
		Live	26–116	33.5–98.0	14.4–102.6	19.4–102.9
>20 to ≤80	Female	Live	—	—	5.0–62.7	5.0–69.7
	Male	Live	—	—	5.0–97.7	5.0–104.9
>80 to 140	Female	Live	—	—	5.0–69.7	5.0–68.0
	Male	Live	—	—	5.0–121.2	5.0–122.6

TABLE 2. *Chionoecetes opilio* ≥25 mm CW in baie Sainte-Marguerite. Mean density estimates for complete exuviae and live males and females in three depth strata sampled by trawl (N_t = number of trawl samples) in March 1988 and 1989 and in April 1990 and 1991. Number of complete exuviae appears in parentheses; see Table 3 for number of live snow crabs.

Year	Depth stratum (m)	N_t	Mean density (no. per 1000 m ²)			
			Male		Female	
			Live	Exuviae	Live	Exuviae
1988	4 to ≤20	1	61.4 ^a	0	3.1	0
1989	4 to ≤20	2	8.2	6.1 (47)	1.6	1.2 (9)
1990	4 to ≤20	6	10.8	49.0 (851)	0.2	0
	>20 to ≤80	3	15.7	0	10.8	0
	>80 to 140	5	17.0	0	34.9	0
1991	4 to ≤20	3	54.7	0	11.1	0
	>20 to ≤80	3	8.6	0	5.0	0
	>80 to 140	3	9.2	0	8.4	0

^aSainte-Marie et al. (1988) estimated that infralittoral density of males prior to the beaching was 122.8–184.2 individuals per 1000 m².

≈40 mm CW. Several 40- to 50-mm CW males were morphometrically mature, and the smallest was 40.4 mm CW (Fig. 2). Many of these males had dirty exoskeletons that were very worn, decalcified, and heavily fouled with epizootes, a condition rarely encountered in morphometrically immature males (B. Sainte-Marie and F. Hazel, unpubl. data). Dissection and histological examination showed that these small morphometrically mature males were also sexually mature; the gonads were relatively large (>1 g formalin-preserved weight), with opaque, convoluted vasa deferentia containing many spermatophores (mature-ripe condition according to Powles 1968 and Watson 1970). The smallest mature female captured in March or April of 1988–91 was 40.8 mm CW and was ovigerous (orange eggs). However, in October 1991, we captured a mature female that measured 39.6 mm CW. None of these very small morphometrically mature males or mature females was deformed or damaged.

Distribution of Live Snow Crabs and Exuviae with Depth

In 1990 and 1991, trawling showed that live snow crabs ≥25 mm CW were present throughout the bay (Table 2). However, males and females with a visible second shell, or exuviae, were found only in the shallow depth stratum (Tables 2 and 3).

Males with clean soft shells were restricted to the shallow stratum, with the exception of only one individual found in the intermediate depth stratum in 1990 (Table 3). Females with clean soft shells were found only in the shallow depth stratum in 1990, but occurred as well in the intermediate and deep strata in 1991 (Table 3). However, none of the primiparous females found at depths >60 m was very recently moulted. Incomplete exuviae, ≈75 in 1989 and ≈780 in 1990, were also found in the shallow depth stratum but not at other depths.

Sex ratios varied with depth for live *C. opilio* and with condition for exuviae. For the shallow depth stratum, the ratio of live males to live females calculated from Table 3 was very strongly biased in favour of males in March 1988 (19.9:1), in March 1989 (5.3:1), in April 1990 (47.0:1), and in April 1991 (5.0:1). Sex ratios were moderately biased in favour of males in the intermediate depth stratum (1.5:1 in 1990, 1.7:1 in 1991) and moderately biased in favour of females or close to unity in the deep stratum (0.5:1 in 1990, 1.1:1 in 1991). Like the sex ratio for live individuals, the male to female ratio for complete exuviae calculated from Table 3 was 5.2:1 in 1989 and 851:0 in 1990. However, most incomplete exuviae were female (≈65% in 1989, ≈95% in 1990).

Our data provide compelling evidence of early spring depth segregation of males by morphometric maturity, shell condition, and size. From 1988 to 1991, the majority of live males in the shallow depth stratum were morphometrically immature (82–96% of males); conversely, the deep stratum was dominated (81–94%) in 1990 and 1991 by morphometrically mature males (Table 4). Morphometrically immature males were the dominant (69%) group of males in the intermediate depth stratum in April 1990, but represented only 19% of males in April 1991 (Table 4). Males in the deep stratum had clean hard or dirty shells, while a mixture of males with visible second shells, clean (soft or hard), and dirty shells occurred in the shallow depth stratum (Table 3). In April 1990 and 1991, morphometrically mature males with hard shells or their exuviae were significantly smaller in the shallow and intermediate depth strata than in the deep stratum (Table 5).

Females also showed a distinct early spring depth segregation by maturity and shell condition. In all years, the majority of females in the shallow stratum were immature or primiparous (99–100%, Table 4), and the latter, with only one exception, had clean soft shells (Table 3). By contrast, in April 1990 and 1991, 95–100% of females in the deep stratum were judged to be multiparous (Table 4). In the intermediate depth stratum, immature and primiparous females accounted together for 50–

TABLE 3. *Chionoecetes opilio* ≥ 25 mm CW in baie Sainte-Marguerite. Frequency of shell conditions (M = moulting, S = soft, H = hard) relative to number of live individuals (N_l) from three depth strata sampled by trawl in March 1988 and 1989 and in April 1990 and 1991.

Year	Depth stratum (m)	Relative frequency (% of N_l)							
		Males				Females			
		M	S	H	N_l	M	S	H	N_l
1988	4 to ≤ 20	11.0	44.9	44.1	537	33.3	48.1	18.5	27
1989	4 to ≤ 20	0.0	55.6	44.4	63	0.0	41.7	58.3	12
1990	4 to ≤ 20	91.5	5.8	2.7	188	25.0	25.0	50.0	4
	>20 to ≤ 80	0.0	0.5	99.5	182	0.0	0.0	100.0	125
	>80 to 140	0.0	0.0	100.0	328	0.0	0.0	100.0	673
1991	4 to ≤ 20	3.9	25.4	70.7	634	0.8	19.5	79.7	128
	>20 to ≤ 80	0.0	0.0	100.0	100	0.0	32.8	67.2	58
	>80 to 140	0.0	0.0	100.0	106	0.0	3.1	96.9	97

TABLE 4. Live *C. opilio* ≥ 25 mm CW in baie Sainte-Marguerite. Frequency of morphometrically immature (Imm) and morphometrically mature (Mat) males and of immature (Imm), mature primiparous (Mat-p), and mature multiparous (Mat-m) females, relative to number of measured individuals (N_m) from three depth strata sampled by trawl in March 1988 and 1989 and in April 1990 and 1991. Number of individuals for which maturity was not determined (N_u) is given.

		Relative frequency (% of N_m)								
	Depth stratum	Males				Females				
Year	(m)	Imm	Mat	N_m	N_u	Imm	Mat-p	Mat-m	N_m	N_u
1988	4 to ≤ 20	86.0	14.0	178	359	81.5	18.5	0.0	27	0
1989	4 to ≤ 20	82.5	17.5	63	0	100.0	0.0	0.0	10	2
1990	4 to ≤ 20	96.1	3.9	180	8	50.0	50.0	0.0	4	0
	<20 to ≤ 80	69.1	30.9	181	1	76.6	23.4	0.0	124	1
	>80 to 140	5.8	94.2	326	2	0.0	0.0	100.0	673	0
1991	4 to ≤ 20	95.5	4.5	595	39	80.5	18.7	0.8	128	0
	<20 to ≤ 80	19.2	80.8	99	1	17.2	32.8	50.0	58	0
	>80 to 140	18.9	81.1	106	0	0.0	5.2	94.8	97	0

TABLE 5. Mean, median, and range of carapace widths of morphometrically mature male *C. opilio* from three depth strata of baie Sainte-Marguerite sampled by trawl in April 1990 and 1991. Results of the Kruskal-Wallis (K-W, H -statistic) analysis of variance by ranks and of Dunn's multiple comparison test are shown. Data are for live hard-shelled individuals and complete exuviae only, i.e. for males that were potentially able to mate with pubescent females during the March breeding period.

Year	Depth stratum (m)	Carapace width (mm)			N
		Mean	Median	Range	
1990	4 to ≤ 20	56.7	55.5	40.4-79.1	10
	>20 to ≤ 80	65.4	62.9	41.3-97.7	55
	>80 to 140	80.2	79.5	49.2-121.2	308
1991	4 to ≤ 20	69.7	71.7	50.3-92.3	15
	>20 to ≤ 80	65.5	63.6	46.0-104.9	80
	>80 to 140	90.8	90.3	52.2-122.6	86

1990 K-W: $H = 41.77$, $P < 0.001$

1991 K-W: $H = 68.82$, $P < 0.001$

Both years Dunn: 4 to ≤ 20 vs. >20 to ≤ 80 , $P > 0.2$
Other pairwise comparisons, $P < 0.05$

100% of all females, and a variety of shell conditions was encountered (Tables 3 and 4).

Sexually Paired Couples in the Field

In March 1991, SCUBA divers collected 136 pairs of snow crabs that were in a pre- or postcopulatory embrace, or in a copulatory position. Divers also collected one recently moulted mature female and two pubescent females with attending males. Additionally, divers observed and collected several small (43–50 mm CW) morphometrically mature males, none of which was paired with another snow crab. Divers noted that when a pubescent female was attended by more than one male, the latter were often fighting. One male held a pubescent female whose outer shell had been crushed by a chela. Two couples were found in which the males held dead, recently moulted mature females that were being consumed by whelks (*Buccinum undatum*). Several other dead females, or immature female exuviae, were seen; their remains were being devoured by lysianassoid amphipods.

Numbers of sexually paired crabs and size composition of females and males in couples did not differ between transects; data were thus pooled for further analyses. Pairs of snow crabs collected by divers fell into five categories. The two most frequent categories were males with pubescent females (77.2% of

TABLE 6. Carapace width (CW), female abdomen width (AW), or male right chela height (CH) for four captive *C. opilio* in the pre- and postmoult conditions. The carapace growth increment (Inc_{CW}) was calculated as the difference between post- and premoult CW divided by premoult CW. Maturity before and after ecdysis is shown in parentheses (Imm = sexually immature females or morphometrically immature male; Mat = sexually mature females or morphometrically mature male). Individuals were collected by SCUBA divers in baie Sainte-Marguerite on 26 April 1991 and moulted overnight.

Sex	Premoult		Postmoult		Inc_{CW} (%)
	CW (mm)	AW/CH (mm)	CW (mm)	AW/CH (mm)	
Female	51.5	25.3 (Imm)	59.8	41.6 (Mat)	16.1
	49.7	24.1 (Imm)	57.7	41.4 (Mat)	16.1
	44.6	23.0 (Imm)	51.9	39.8 (Mat)	16.4
Male	82.7	14.8 (Imm)	97.9	22.9 (Mat)	18.4

136 pairs) and males with recently moulted mature females that either were ripe, ovipositing, or already berried (10.3%). The third category, represented by only one pair (0.7%), consisted of a male (89.8 mm CW) with a multiparous female (60.3 mm CW). These three categories were collectively called potentially fecund couples. The fourth category involved males that were paired with other males (7.4%), and the fifth category (4.4%) grouped males that were paired with immature sterile females. These two latter categories were collectively called sterile couples.

The distribution of carapace widths of sexually paired pubescent females did not differ significantly from normality (Kolmogorov-Smirnov test, $\text{DN} = 0.04$, $P > 0.99$); mean ($\pm$ SD) carapace width was 49.4 ± 3.3 mm ($N = 105$). Similarly, carapace widths of recently moulted mature females conformed to normality (Kolmogorov-Smirnov test, $\text{DN} = 0.17$, $P > 0.99$) with a mean of 59.0 ± 3.6 mm ($N = 15$). Thus, under the reasonable assumption that these two modes represented consecutive moult instars, the mean growth increment for pubescent females moulting to maturity in nature was 19.4%. This value is slightly greater than the average 16.3% increment derived for three pubescent females that moulted to maturity in captivity (Table 6). However, in the field, the only live primiparous female that could be unambiguously associated with an exuvia, because the pattern of missing and incompletely regenerated pereopods was the same on both, showed an increase of just 11.7% (exuvia = 51.4 mm CW, postmoult female = 57.4 mm CW). This female and those that moulted in captivity were still very soft, so more carapace growth was expected because our laboratory observations have shown that up to 2 d is required following ecdysis for carapace to reach full width. The growth increment for the captive male, during its moult to morphometric maturity, was 18.4% (Table 6). Again, because this male was still in a very soft condition at the time of measurement, the calculated growth increment may be considered a minimum value.

All but four males in potentially fecund couples (96.7% of 120 males), all of the males attending females (100% of 6), and all but two grasping males in sterile couples (87.5% of 16) were morphometrically mature. In potentially fecund couples, 13.3% of males lacked one chela, while one male (0.8%) lacked both chelae but held one of the female's pereopods firmly wedged between the flexed dactyl and propodite of his second left walking pereopod. In sterile couples, 6.3% of grasping males lacked one chela. In the 10 male-male pairs, four of the

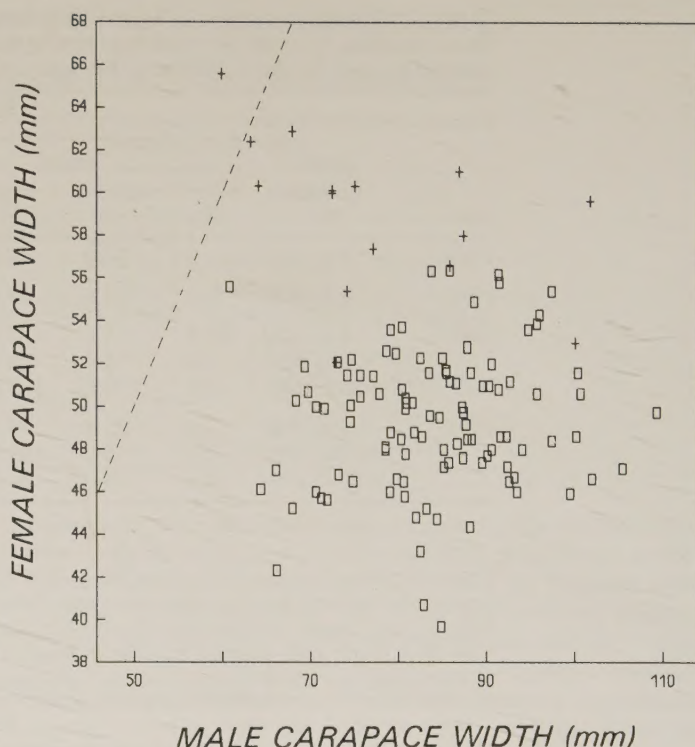


FIG. 3. Carapace widths of males and females ($\square$, pubescent; +, mature) in potentially fecund couples of *C. opilio* collected by SCUBA divers at ≤ 35 m in baie Sainte-Marguerite in March 1991. The oblique broken line represents a 1:1 ratio of male to female size.

submissive males lacked one or both chelae and six were severely battered, with freshly broken limbs.

In potentially fecund couples, only 11.7% of males were ≥ 95 mm CW and, with only one exception, carapace width of males was always larger than that of females (Fig. 3). One recently moulted mature female was larger than her mate but, assuming the couple was formed prior to female moult and considering the calculated mean growth increment for pubescent females (see above), it is highly probable that prior to moulting, this female was smaller than the male. There was no correlation between the sizes of grasping males and pubescent females ($r = 0.10$, $P > 0.1$), and the negative correlation between the sizes of grasping males and of soft-shelled mature females was marginally not significant ($r = -0.50$, $P = 0.06$). There was no correlation between depth and carapace width of males in potentially fecund couples ($r = 0.08$, $P = 0.39$). Grasping males in sterile couples (Fig. 4, $N = 16$, mean $\pm$ SD: 68.2 ± 11.3 mm CW, range: 43.1–83.4 mm CW) were also larger than their mates, but were significantly smaller (t -test: $t = 5.53$, $P < 0.001$) than males in potentially fecund couples ($N = 120$, mean $\pm$ SD: 83.2 ± 10.0 mm CW, range: 59.9–109.3 mm CW).

Maturity of *C. opilio* at Moulting

The large number of complete exuviae and of live *C. opilio* committed to moult provided a unique opportunity to determine the incidence of moulting in males and females as a function of maturity. In doing so, we restricted analyses to consider only complete exuviae and live individuals ≥ 40 mm CW, i.e. the minimum size at male morphometric and female sexual maturity.

Morphometrically mature males seldom moulted. Considering complete male exuviae, those classified as morphometri-

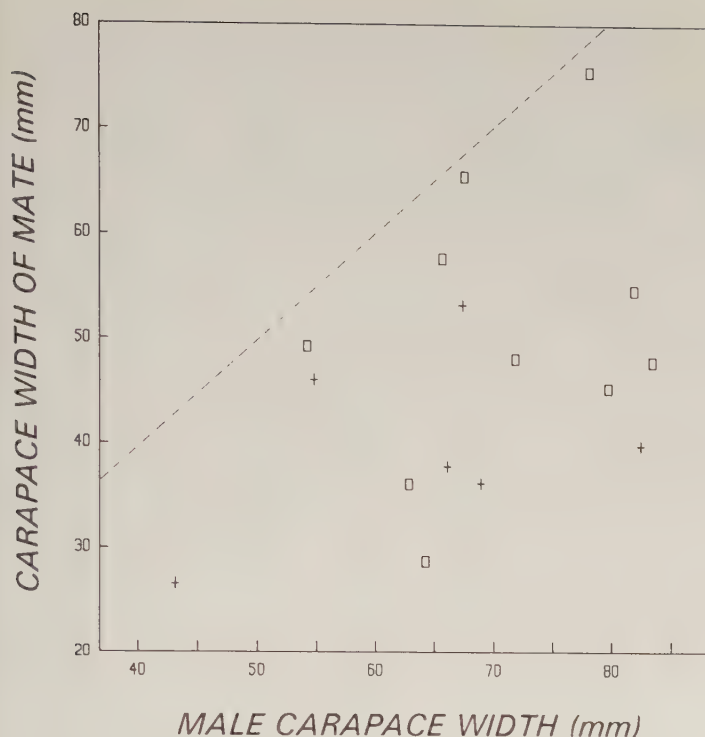


FIG. 4. Carapace widths of male *C. opilio* grasping other males (□) or immature sterile females (+) collected by SCUBA divers at ≤ 35 m in baie Sainte-Marguerite in March 1991. The oblique broken line represents a 1:1 ratio of male to mate size.

cally mature never represented more than 8% (2 of 25 exuviae in 1989) of the total (Table 7). Overall, morphometrically mature males represented only 1.9% of 424 complete male exuviae measured in 1989 and 1990. Moreover, most of these morphometrically mature male exuviae were small and lay very close to the cutting line (Table 7). Rather than consider the exuviae record, a biologically more meaningful analysis is to consider moulting frequency relative to total population of males that could potentially moult (i.e. all but soft-shelled males) in each category of morphometric maturity (Dawe et al. 1991). Four consecutive years of visual examination of all males that could potentially moult showed that the relative frequency of individuals with a visible second shell varied from 0 to 0.5% for morphometrically mature males compared with 0 to 54.4% for morphometrically immature males (Table 7). From 1988 to 1991, excluding soft-shelled males, a mere 0.3% (two small individuals) of 575 morphometrically mature males compared with 23% of 826 morphometrically immature males sampled in early spring had a visible second shell and were thus committed to moult. Carapace width of the largest morphometrically immature males with a second visible shell was 102.9 mm.

The above estimates of numbers of male *C. opilio* committed to moult may be conservative because individuals in very early stages of ecdysis cannot be detected by visual inspection. In April 1991, dissection and determination of moult stage were used to further ascertain relative frequency of moulting in either category of morphometric maturity (Table 7). Combined data from dissection and moult stage, exclusive of soft-shelled males, revealed that none of the 88 clearly morphometrically mature males was preparing to moult, while 48.5% of 66 clearly morphometrically immature males were double-shelled or in D_0 – D_4 stages. The complete breakdown of moult stages determined for the 43 morphometrically immature males was

the following: 39.5% in C, 4.7% in D_0 , 30.2% in D_1 , 9.3% in D_3 – D_4 , and 16.3% in A–B. The estimated frequency of morphometrically immature males for which moulting was imminent, relative to total population of morphometrically immature males, was not independent of method (visual, 5.4%; dissection, 43.3%; moult stage, 52.8%: $G_{adj} = 70.5$, $df = 2$, $P < 0.001$).

There was no evidence that mature females moulted, but the recorded frequency of moulting of immature females was also very low. From 1988 to 1991, females with a visible second shell represented 4.9% of 163 immature and 0% of 457 mature females, excluding those with soft shells. All complete female exuviae ($N = 9$) were immature, as were all incomplete exuviae ($N \approx 49$ in 1989, $N \approx 740$ in 1990) judging from the imprint of the abdomen on the thoracic sternites; we are, however, uncertain that all of the latter were ≥ 40 mm CW. All diver-collected females ($N = 107$) that were committed to moult had immature external features.

Discussion

Occurrence and Moulting of *C. opilio* in Shallow Waters

From 1988 to 1991, the shallow grounds of baie Sainte-Marguerite were occupied by *C. opilio* in early spring, as hypothesized by Sainte-Marie et al. (1988). The occurrence of *C. opilio* in the shallows is clearly a seasonal event because sampling has demonstrated that snow crabs were absent from those grounds in late May, June, and August of 1990 and 1991 (B. Sainte-Marie and S. Raymond, unpubl. data). Downslope movement away from the infralittoral zone may be linked to the gradual warming of surface waters, to maxima of 10–16°C in summer, beyond lethal temperatures for *C. opilio* (Foyle et al. 1989). A definite time for the appearance of *C. opilio* in the shallows is not yet determined.

The infralittoral grounds of baie Sainte-Marguerite were apparently the only site for moulting of males ≥ 25 mm CW. Indeed, when all depth strata were sampled in 1990 and 1991, males with a visible second shell and exuviae were found exclusively on the shallow bottoms (Tables 2 and 3). The depth distribution of moulting females was slightly more extensive, as evidenced by 1991 diver collections of moulting females in the intermediate depth stratum. Anecdotal observations suggest that shallow-water moulting has, at least in recent years, been a widespread phenomenon for coastal populations of *C. opilio* in the Gulf of Saint Lawrence. In early May 1989, we found soft-shelled males (64–113 mm CW) on shallow (< 20 m) sandy bottoms of the Mingan Archipelago (Fig. 1), while Ennis et al. (1990) discovered numerous cast shells (53–104 mm CW) at depths of 20–35 m in Bonne Bay, Newfoundland. Pointe-aux-Anglais (Fig. 1) was the site of a small beaching of snow crabs in late March 1991 (É. Mauger, Department of Fisheries and Oceans, Sept-Îles district, pers. comm.), in all respects similar to the earlier beaching in baie Sainte-Marguerite (Sainte-Marie et al. 1988). A very large beaching of male *C. opilio* was also reported from the coast of remote Anticosti Island (Fig. 1) in the early spring of 1991 (J. Landry, Havre Saint-Pierre, pers. comm.), but condition and size of crabs were not determined. Based on our experience, however, it seems unlikely that hard-shelled males were involved; we therefore assume that stranded males were recently moulted. Lastly, in early April 1991, L. Gendron (Institut Maurice-Lamontagne, pers. comm.) found concentrations (mean density: 164.7 individuals per 1000 m² based on three tows with a beam trawl) of moulting or recently moulted female and male snow crabs

TABLE 7. Male *C. opilio* ≥ 40 mm CW in baie Sainte-Marguerite. Relative frequency of exuviae and of live individuals (Freq., in %) committed to moult for morphometrically immature (Imm) and morphometrically mature (Mat), relative to total number of measured exuviae (N_e) or number of live males exclusive of soft-shelled (N_s). Frequency of moulting was determined either by visual examination to detect double-shelled individuals, dissection to detect underlying shells, or determination of moult stage. Males were collected by trawl in March 1988 and 1989 and in April 1990 and 1991. Carapace width (CW_{obs} , in mm), right chela height (CH_{obs} , in mm), and difference between natural logarithm of CH_{obs} and of CH on cutting line ($\ln CH_{line} = 1.2209 \ln CW_{obs} - 2.6077$) are given for exuviae or moulting individuals classified as morphometrically mature.

Year	Depth of samples (m)	Male exuviae			Live males committed to moult			
		Imm	Mat	N_e	Method	Maturity	Freq.	N_s
1988	4 to ≤ 20	—	—	0	Visual	Imm	6.6	121
						Mat	0.0	23
1989	4 to ≤ 20	92.0	8.0 ^a	25	Visual	Imm	0.0	19
						Mat	0.0	4
1990	4 to 140	98.5	1.5 ^b	399	Visual	Imm	54.4	296
						Mat	0.5 ^c	367
1991	4 to 140	—	—	0	Visual	Imm	5.4	390
						Mat	0.0	181
					Dissection	Imm	43.3	30
						Mat	0.0	48
					Moult stage	Imm	52.8	36
						Mat	0.0	40

Measurements, morphometrically mature (CW, CH, $\ln CH_{obs} - \ln CH_{line}$):

^a47.6, 8.5, 0.03; 59.4, 10.9, 0.01.

^b40.4, 7.3, 0.08; 41.2, 7.8, 0.12; 43.9, 8.2, 0.09; 49.9, 9.1, 0.04; 68.7, 13.0, 0.01; 79.1, 15.5, 0.12.

^c52.4, 10.3, 0.11; 71.9, 15.2, 0.11.

(18–93 mm CW) at depths of 25–32 m on the north shore of baie des Chaleurs (Fig. 1).

Our findings provide direct support for an earlier hypothesis that recruitment of males to deep coastal fishing grounds occurs following a downslope movement of recently moulted males (Coulombe et al. 1985; Bouchard et al. 1986). This hypothesis was derived from observations of temporal changes in the size composition of snow crabs on commercial fishing grounds. Downslope movements of morphometrically mature male *C. opilio* have been documented (Lefebvre and Br  thes 1991). Thus, in our study, the existence of large morphometrically immature males (103 mm CW) that were committed to moult in the shallows, a potential growth increment of 18–19% (Table 6), and a subsequent downslope movement can account for the presence of the largest morphometrically mature males (121–123 mm CW) in deep areas of baie Sainte-Marguerite.

Observations of *C. opilio* in shallow waters modify our perception of this species' bathymetric distribution. On the eastern coast of Canada, the general picture of snow crab distribution with depth, in reality more a function of temperature and (or) possibly sediment characteristics (Coulombe et al. 1985; Br  thes et al. 1987), was derived only from summer and fall observations. At those times, snow crabs are confined to bottoms bathed by waters $< 3^\circ\text{C}$, at depths exceeding 40 m (Brunel 1961; Coulombe et al. 1985; Br  thes et al. 1987). The shallow-water populations of *C. opilio* were at times substantial (Table 2); the upper mean estimates for male density in the shallow depth stratum of baie Sainte-Marguerite (57 and 184 males per 1000 m²) were about one order of magnitude greater than those for males in deeper areas of the bay (9–17 males per 1000 m²) and than previously published estimates for similarly sized males at other sites (reviewed in Robichaud et al. 1989).

Why *C. opilio* move onto shallow grounds is unclear. A variety of decapod Crustacea, including at least two other majid

crabs, *Maja squinado* (Carlisle 1957) and *Libinia emarginata* (DeGoursey and Stewart 1985; DeGoursey and Auster 1989) also move into shallow waters, apparently for the purpose of moulting. Predation and (or) cannibalism have often been invoked as likely factors in the spatial segregation of moulting and nonmoulting individuals of decapod crustaceans (e.g. Carlisle 1957; Lipcius and Herrnkind 1982; Hines et al. 1987; Ryer et al. 1990; Shirley et al. 1990). In the Gulf of Saint Lawrence, important predators of soft-shelled *C. opilio* are Atlantic cod (*Gadus morhua*) and thorny skate (*Raja radiata*) (Robichaud et al. 1991), both of which are common in the intermediate and deep strata but absent from the shallow depth stratum of baie Sainte-Marguerite (B. Sainte-Marie, unpubl. data). Also, cannibalism of soft-shelled male *C. opilio* by large hard-shelled males has been documented (Watson 1971), and aggressive male interactions resulting in bodily harm have been reported during the spring breeding season for *C. bairdi* and *C. opilio* (Watson 1970; Hooper 1986; Donaldson and Adams 1989). A retreat to shallow waters prior to moulting would thus provide vulnerable (recently moulted) males with refuge from cod, skate, and large male congeners. If these incursions into shallow water are only recent events, however, they may reflect a density-dependent response related to the apparent increase of snow crab populations throughout the Gulf of Saint-Lawrence, suggested over the past 2 yr by growing fishery yields in several fishing zones.

Early spring appears to be the main period for moulting of *C. opilio* in baie Sainte-Marguerite, as has been inferred for other localities of eastern Canada (Miller and O'Keefe 1981; Moriyasu et al. 1987; Conan et al. 1990). From 1988 to 1991, a majority of morphometrically immature males and of immature females ≥ 25 mm CW of *C. opilio*, sampled by trawl in baie Sainte-Marguerite, were committed to moult or had

recently moulted (Tables 3 and 7). Moreover, our estimates of the number of individuals committed to moult relative to total population of morphometrically immature males, exclusive of soft-shelled individuals, are certainly conservative for 1988–90 (when they were based only on visual examination of individuals), as evidenced by the significant impact of methodology on 1991 estimates. We point out, however, that moulting of *C. opilio* <25 mm CW is not confined only to the late winter through early spring period (S. Raymond and B. Sainte-Marie, unpubl. data), as inferred by Robichaud et al. (1989).

Laboratory studies by Moriyasu et al. (1987) suggested the existence of more or less discrete moulting periods for different groups of *C. opilio* in the Gulf of Saint Lawrence: early February for immature females that moult to maturity and late February through late April for immature females that moult to a further immature stage and for males moulting to a further morphometrically immature or to a morphometrically mature stage. In 1989 and 1990, the biased sex ratios in favour of female incomplete (i.e. weathered) exuviae and the biased sex ratio in favour of male complete (i.e. recent) exuviae and moulting individuals indicate temporal segregation of moulting activity on the shallow grounds of baie Sainte-Marguerite, with females moulting prior to males. Our observation of immature females moulting to maturity in late March 1991 implies that there is more regional and (or) year-to-year variation in the timing of the moult than was hitherto recognized.

Mating of Pubescent Females

Pubescent females mated with morphometrically immature and morphometrically mature males 59.9–109.3 mm CW, a majority (88.3%) of which were <95 mm CW (Fig. 3). These field observations do not prove that the matings resulted in viable broods, but in the laboratory, pubescent females mated with morphometrically immature (most of which moulted shortly after mating) or morphometrically mature males ≥ 47 mm CW and produced broods that developed into prezoe larvae (B. Sainte-Marie, unpubl. data). It thus is reasonable to conclude that males <95 mm CW, both morphometrically immature (with functional gonads) and morphometrically mature, can successfully mate pubescent females in the field. Morphometrically mature males, however, represented 97% of all males paired with potentially fecund females (Fig. 3). As argued for other species with sexually mature, small- and large-clawed morphs, e.g. the amphipod *Jassa falcata* (Borowsky 1985) and the decapod *Orconectes rusticus* (Snedden 1990), large chelae or traits associated with large chelae (e.g. greater aggressiveness) likely confer a decisive advantage in competitive mating situations. Males were always larger than their pubescent female mate (Fig. 3), as reported for *C. bairdi* (Brown and Powell 1972).

Some grasping male *C. opilio* (16 of 136 observed) were engaged in activities with a mate for which brooding was impossible, i.e. another male or an immature sterile female. This implies that some males were not readily able to discriminate pubescent females from other crabs. Receptive *C. opilio* females may signal their presence by way of pheromones (Hooper 1986), as other crustacean decapods do (e.g. Ryan 1966; Atema and Engstrom 1971; Christoffersen 1978). Sex pheromones of *Carcinus maenas*, emitted by females in short pulses, are effective only over a very short horizontal range of 10–20 cm and are not species specific (Seifert 1982); the same characteristics in *C. opilio* might result in mispairings. However, because grasping *C. opilio* males in sterile couples also

were significantly smaller than those in potentially fecund couples, an alternative or complementary explanation for the existence of mispaired couples is that pubescent females were a limited resource. This is substantiated by the observations that (1) males fought for pubescent females, (2) they invested in these females by carrying them prior to moulting and then watched over them until they had extruded their eggs and hardened, the whole process lasting up to several days, and (3) very small (<59.9 mm CW) morphometrically mature males, present on the grounds as determined by divers and trawl, did not mate with pubescent females despite their ability to do so in a non-competitive laboratory environment. The latter point agrees with data for two other majid crabs: sexually paired males were significantly larger than solitary mature males in *Inachus phalangium* (Diesel 1988) and than the overall male population in *L. emarginata* (DeGoursey and Auster 1989). Our data thus invalidate statements that morphometrically mature males <95 mm CW rarely mate with pubescent females (Conan and Comeau 1986) and that there is no male competition for pubescent females (Conan et al. 1990).

The observed early spring spatial segregation of males, by size (Table 5), and of females, by reproductive experience (Table 4), could have important consequences for reproduction of *C. opilio*. Larger, morphometrically mature males with hard shells remained in deep areas of the bay, where they would mate with multiparous females. Pubescent females, however, were courted principally by smaller morphometrically mature males that concentrated in the shallows. Depth segregation of males by size and of females by reproductive experience is a common feature of *Chionoecetes* (Pereyra 1966; Kon 1969), leading to Somerton's (1982) proposed bipartite reproductive scheme for *C. opilio elongatus*. Assortative mating could result in distinct progenies for the primiparous and multiparous females, particularly if male size at morphometric maturity is genetically determined. The possibility that differences exist in the quantity (Haynes et al. 1976; Somerton and Meyers 1983) and quality (genotype, condition, and survivorship) of progeny descended from primiparous and multiparous females should be thoroughly investigated.

Terminal Moulting Hypothesis

Is there a terminal moult in *C. opilio* that coincides with morphometric maturity in males? Various laboratory studies have attempted to resolve this question (Cormier 1986; Moriyasu et al. 1987; O'Halloran et al. 1988; Bataller et al. 1989), but in our opinion, estimates of moulting frequency for morphometrically immature and morphometrically mature males in nature are definitive. Unfortunately, because changes in the size of chelae of males are rather subtle (Fig. 2), and for lack of unambiguous criteria (analogous to shape of abdomen or presence of brood for females), classification of males into either category of morphometric maturity is uncertain.

Notwithstanding biological and statistical problems involved in determining male morphometric maturity, our observations show that moulting of morphometrically mature males was a very rare event and thus support the terminal moult hypothesis. Based on visual detection of a second shell, the relative moulting frequency was 26.5% ($N = 686$) for morphometrically immature males and 0.4% ($N = 548$) for morphometrically mature males. This estimate is exclusive of males with soft shells and is for two consecutive years (1990 and 1991) when the whole population (4–140 m) of baie Sainte-Marguerite was sampled. Exuviae records of moulting activity, for baie Sainte-Marguerite (Table 7) and Bonne Bay (Ennis

et al. 1990), also support the view that morphometrically mature males rarely moult. Also, estimates of relative moulting frequency of hard-shelled males that lay clearly above and below the cutting line in Fig. 2, in 1991, using more refined methods, were even more contrasting: 48.5% of the morphometrically immature males and none of the morphometrically mature males were committed to moult (data from dissection and moult stage, pooled). Our observations are not liable to any of the five major criticisms (sampling in only 1 yr and not coincident with time of moult, shell condition not specified, males collected by trap, no morphometrically mature or immature moulting males) directed by Dawe et al. (1991) at previous attempted demonstrations of the existence, in nature, of a terminal moult. Some of these criticisms still pertain, however, to a recent, attempted demonstration of the existence of a terminal moult for male *C. opilio japonicus* (Yamasaki and Kuwahara 1991). We continue to monitor the baie Sainte-Marguerite population to confirm the seasonal and synchronous nature of moulting in males and to determine year-to-year variations in the moulting frequency of morphometrically mature males.

Some males classified as morphometrically immature were so irreversibly deteriorated, with dirty and decalcified exoskeletons, numerous epizootes and scars, and badly necrosed gills, that their terminal moult status was undoubtful. For these males, measurement of the left chela revealed a striking size asymmetry between chelae because the right was incompletely regenerated (Fig. 2) and they were determined to be morphometrically mature with respect to the left chela. While measurement of the left chela can dispel uncertainty as to the real morphometric status of some males, there are other cases where both chelae are missing or incompletely regenerated.

The minimum body size at sexual maturity of females (39.6 mm CW) and at morphometric maturity of males (40.4 mm CW) was less in baie Sainte-Marguerite than elsewhere. Previously reported minimum values were 52 mm CW for males (Conan and Comeau 1986) and 40.3 mm CW for females (Jewett 1981). Possible reasons for these differences include negative fishery selection on size at morphometric maturity (Elner et al. 1986; Bailey and Elner 1989), oversight of previous investigators, regional variability, and interannual trends in size at morphometric maturity.

Conclusions

Chionoecetes opilio have moved onto shallow grounds of baie Sainte-Marguerite for the last 4 yr. Anecdotal evidence suggests that early spring occurrence of *C. opilio* on shallow grounds is quite common in the northern Gulf of Saint-Lawrence. Pubescent females were mated in the shallows, mainly by small morphometrically mature males; multiparous females were probably mated on deeper grounds by larger males. Data indicate that mature females are terminally moulted and that morphometrically mature males rarely moult. For males, extreme reduction of moulting frequency, or terminal moult, has two immediate implications: total mortality of morphometrically mature males can be calculated, but medium to long-term prediction of harvestable biomass by assessment of pre-cruits is compromised. Elucidating factors that govern the moult to morphometric maturity and predicting its onset thus represent major challenges of snow crab research.

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Statistical Evaluation of a Large-Scale Fishing Experiment Designed to Test for a Genetic Effect of Size-Selective Fishing on British Columbia Pink Salmon (*Oncorhynchus gorbuscha*)

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Since 1950, stocks of British Columbia pink salmon (*Oncorhynchus gorbuscha*) have shown up to a 34% decrease in mean adult body weight, causing significant reduction in economic value of commercial harvests. Previous research suggests that this trend is due to size-selective harvesting of large fish, but changes in oceanographic conditions are a plausible alternative. Corrective action by management agencies requires that the true causal mechanism be identified. We therefore examined several possible designs for a large-scale fishing experiment devised to test the size-selective fishing hypothesis. These designs would generate accurate and precise field estimates of the heritability (h^2) of growth rate, which is important because it, in combination with the selection differential (D) caused by fishing, determines how rapidly body size changes. Monte Carlo simulations showed that block designs with three to six spatial replicates and relatively short durations generated high statistical power. For example, for $h^2 = 0.22$, $D = 0.25$ kg, and four spatial replicates, an 8-yr experiment resulted in power = 0.87, which gave a $SE < 0.10$ for $h^2 = 0.22$. We conclude that some experimental designs have good potential to test the possible effects of size-selective fishing on mean adult size of British Columbia pink salmon.

Depuis 1950, le poids moyen des adultes des saumons roses (*Oncorhynchus gorbuscha*) de la Colombie-Britannique a diminué d'une valeur pouvant atteindre 34 %, ce qui s'est traduit par une réduction appréciable de la valeur des prises commerciales. Les résultats d'études antérieures portent à croire que cette tendance résulte d'une pêche sélective des plus gros poissons, mais des changements des conditions océanographiques pourraient aussi expliquer ce phénomène. La prise de mesures correctives de la part des organismes de gestion suppose la détermination du mécanisme réellement à l'origine de cette baisse de poids. Nous avons donc examiné diverses configurations d'une expérience de pêche à grande échelle conçue de façon à tester des hypothèses de pêche sélective. Ces configurations devaient permettre d'obtenir des estimations exactes et précises de l'héritabilité (h^2) du taux de croissance. Ce facteur est important car il détermine, de pair avec l'écart de la sélectivité (D) par pêche, le taux de variation de la taille des poissons. Des simulations Monte Carlo ont montré que des configurations d'ensembles comportant de trois à six répétitions spatiales et de durée relativement courte permettaient d'obtenir une puissance statistique élevée. ainsi, pour $h^2 = 0,22$, $D = 0,25$ kg et quatre répétitions spatiales, une expérience d'une durée de 8 ans donne une puissance de 0,87, soit $ET < 0,10$ pour $h^2 = 0,22$. Nous en concluons que certaines configurations expérimentales constituent un bon moyen de vérifier les effets d'une pêche sélective quant à la taille sur la taille moyenne des saumons roses adultes de la Colombie-Britannique.

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Poor understanding of the population dynamics of renewable resources can result in reduced economic benefits through incorrect choice of management regimes. This has led several authors to advocate an experimental approach to management that would test hypotheses about the components of natural resource systems while identifying optimal management regimes (Larkin 1972; Walters and Hilborn 1976, 1978; Peterman and Routledge 1983; Ludwig and Hilborn 1983; Lee and Lawrence 1986; Walters 1986; Walters et al. 1988, 1989; Sainsbury 1988; Walters and Collie 1989; McAllister and Peterman 1992a). In this paper and its companion (McAllister

and Peterman 1992b), we propose a large-scale fishing experiment and evaluate its potential to test one of the major hypotheses concerning the decreasing mean adult body size of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia (B.C.). We report the expected statistical performance of experimental designs in this paper and their economic performance in the companion paper.

Since the 1950s, several stocks of adult pink salmon in B.C. have shown up to a 34% decrease in mean body weight (Ricker et al. 1978) (Fig. 1). This decrease is not attributable to a shift in age at maturity because virtually all pink salmon in B.C. mature at age 2 yr. Decreased fish size is a problem for fisheries managers for several reasons. First, decreased mean adult size can result directly in decreased catch biomass (e.g. a 34% decrease in mean adult body weight corresponds to a potential

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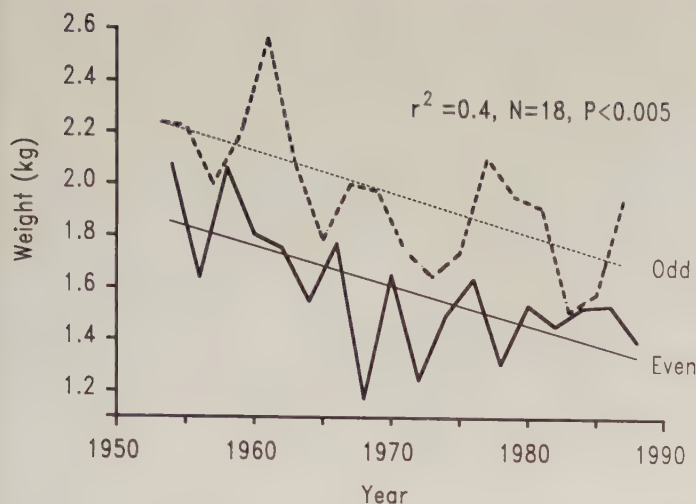


FIG. 1. Mean adult weight of pink salmon in even- and odd-numbered years in B.C. statistical area 7 for years 1953–88. Values shown for r^2 , N , and P were the same for even- and odd-year stocks.

34% decrease in catch biomass if the number of fish caught remains the same). Second, decreases in mean adult body size may also affect reproductive success. A growing body of evidence suggests that large female body size confers substantial reproductive advantages in salmon. Larger female pink salmon carry more and larger eggs (Foerster and Pritchard 1941; Bilton 1973) and may spawn earlier, resulting in increased freshwater survival of offspring (Skud 1973). Similarly, large female coho salmon (*O. kisutch*) (1) obtain better nest sites, (2) dig deeper redds that are less vulnerable to scouring, and (3) defend nests longer, reducing the risk of egg dig-up by other spawners (van den Berghe and Gross 1989). Furthermore, smaller pink salmon may be less able to swim long distances or up steep gradients to spawning grounds (Ricker 1989). Thus, there may be a reproductive disadvantage for smaller than average size adults, especially females, and reduced mean adult weight could thereby reduce stock productivity (Foerster and Pritchard 1941).

Most B.C. pink salmon stocks showed a strong decreasing trend in mean adult weight between 1959 and 1975 (Ricker et al. 1978). Since 1975, some of these stocks have continued to decrease while others have not (Healey 1986). This recent pattern has created controversy about the causes of interannual variation in mean body size of pink salmon. Ricker et al. (1978) hypothesized that the decreasing trends in body size of B.C. pink salmon resulted from removal of larger than average size fish by fishing gear, combined with heritability of growth rate (h^2). However, the trend in mean adult body size could also have resulted from changes in oceanographic conditions (Healey 1986), increased intra- or interspecific competition (Healey 1986; Peterman 1987), or selective depletion of stocks with larger mean body size (interstock selection) (Nelson and Soule 1987). Note that because pink salmon enter the ocean at a very small body size (<1 g) and mature about 16 mo later at approximately 1.5–2 kg, observed trends in adult body size are almost completely determined by growth rate during the marine life phase. Hence, we refer to heritability of growth rate, not heritability of body size.

Current data do not enable us to reject any of the above hypotheses (M. K. McAllister, R. Lockhart, and R. M. Peterman, unpubl. data) because estimates of h^2 from historical catch data (e.g. Ricker et al. 1978) are potentially confounded with selective depletion of larger stocks, or oceanographic and density-dependent effects. Interpretations of past data are also con-

strained by a lack of spatial controls to compare with selectively fished stocks (no nearby pink salmon stocks were fished entirely with nonselective gear such as purse seines). Furthermore, although Beacham and Murray (1988) estimated an h^2 of 0.1–0.3 for male and 0.4–0.8 for female pink salmon from the Quinsam River, B.C., their estimates were from artificially raised pink salmon. The samples therefore do not represent the full range of additive genetic variance and natural environmental effects on phenotypic variation that contribute to h^2 in wild populations. Thus, their experimental estimates are probably overestimates for wild populations because of the relatively controlled experimental environment compared with the wild situation ($h^2 = (\text{additive genetic variance})/(\text{total variance including environmentally caused variance})$, Falconer 1989). Note that estimates of h^2 from hatchery experiments that involve release of offspring of selected parents into the wild could result in either over- or underestimates of h^2 in wild populations. Underestimates could result from a reduction in genetic variance from selective breeding (e.g. of the largest individuals) in the past. Overestimates could result from former practices of combining different brood stocks in the same hatchery.

Defining Management Alternatives

Given the importance of decreased body weight of B.C. pink salmon, management options should be explored to rectify the problem. First, managers could adopt the status quo, which is to continue size-selective harvesting of large fish and hope that (a) oceanographic conditions are the cause of the past trend and (b) those conditions will reverse themselves. As noted above, this management policy has potentially large costs if the cause is actually size-selective fishing. Second, managers could impose new fishing regulations requiring the use of selectively neutral gear to let natural selection slowly increase body size (e.g. ban gill nets and troll gear and permit the use of purse seines only). Third, managers could attempt to increase mean adult body size more rapidly through regulations that lead to size-selective harvest of *smaller* fish. The latter two alternatives might resolve the problem of reduced adult body size, but if the measures did not work, they would result in continued uncertainty and unnecessary costs and inconvenience to fishermen. Even if mean body size increased, the lack of a rigorous experimental design (replicated controls and treated stocks) could lead to continued uncertainty over the cause(s) of the increase, which might or might not be associated with changes in fishing regulations. Therefore, a fourth alternative is to implement the latter regulations that selectively harvest smaller size fish, but in a rigorously designed large-scale fishing experiment (Hurlbert 1984). Regardless of whether body size increases, this experimental strategy will reduce uncertainty about the cause of changes in body size because one or more alternatives can be tested rigorously. With an experimental option, managers could expect a greater chance of eventually identifying the best long-term policy than with any nonexperimental alternative (Walters 1986). Furthermore, if size-selective fishing is the cause of the historical decline, this fourth option has the potential to rapidly increase body weight, with obvious biological and economic benefits.

An experimental strategy should help to resolve uncertainty about the size-selective fishing hypothesis by permitting a good field estimate of h^2 , an index of the potential for mean adult body weight to change in response to such fishing. In order for size-selective fishing to induce evolutionary changes in mean adult weight of pink salmon, directional selection must occur

and h^2 must be >0 (Falconer 1989). Ricker et al. (1978) showed that troll and gillnet gear cause directional selection by harvesting larger than average size fish, but as noted above, no reliable estimates of h^2 exist for wild pink salmon populations. Therefore, a carefully designed experiment in which h^2 was estimated reliably could help managers considerably.

Criteria for Evaluating Designs

There are many potential experimental designs and not all will be equally informative. For instance, some will have too few replicate stocks or too short a duration to estimate heritability in body size well, even if h^2 is large. Thus, a range of alternative designs must be evaluated.

We used two criteria, accuracy and precision of parameter estimates, plus statistical power (Dixon and Massey 1983; Toft and Shea 1983) to evaluate the potential of alternative experimental designs to test the gear selectivity hypothesis on B.C. pink salmon. In a companion paper, McAllister and Peterman (1992b) used a third approach, decision analysis, to compare the best and most feasible of these experimental designs with the status quo management policy in terms of the expected economic value of harvested biomass. The accuracy and standard error (SE) of an estimated parameter (here of h^2) is a common means of comparing performance of different experimental designs (Walters et al. 1988). A priori statistical power analysis has also been used in such comparisons (Green 1979, 1989; Peterman and Routledge 1983; de la Mare 1984; Cohen 1988; Peterman 1990) because it can quantify the probability that the experiment will reject the null hypothesis, H_0 , if it is carried out when H_0 is indeed false. In our example, this means that if we simulate a situation in which $h^2 > 0$, the best experimental design would be the one with the highest power (e.g. > 0.8), or probability of rejecting the H_0 of $h^2 = 0$, using a one-tailed t -test. Power depends on the sample size, size of the true effect (here the value of h^2), and sample variance (Cohen 1988).

Analyses of historical data show that values for h^2 would have to be in the range of 0.18–0.25 in order for size-selective fishing to account for the historical decrease in mean adult body weight in B.C. pink salmon (Ricker et al. 1978; McAllister 1990). Therefore, in the simulations described below, we assumed that the real value of h^2 was between 0.18 and 0.25. Through Monte Carlo simulation of time series of body weights, we then evaluated different experimental designs by comparing their probabilities of correctly rejecting the null hypothesis of $h^2 = 0$. Clearly, a design that had a low probability when the simulated true h^2 was between 0.18 and 0.25 would not be useful in the field for determining the importance of size-selective fishing. We explored experimental designs with different durations, number of spatial replicates, values for selection differential, h^2 , and chance variation.

Methods

Statistical Model

The statistical model used to estimate h^2 from a set of experimental data should also be used for a priori statistical power analysis of potential experimental designs (Peterman 1990). The following model represents the various components of interannual variation in mean adult weight of pink salmon that may be present in a size-selective fishery:

$$(1) \quad W_{i,t} - W_{i,t-2} = B_0 + T_t + h^2 D_{i,t-2} + E_{i,t}$$

where $W_{i,t}$ is the mean adult body weight just prior to fishing of stock i in year t of the experiment. Each stock i consists of either a single even-year or odd-year breeding population of pink salmon caught in the same terminal fishery (i.e. a fishery located adjacent to the mouth of a spawning stream). $W_{i,t-2}$ is the mean adult body weight just prior to fishing of the parental generation of stock i in year $t - 2$ of the experiment. B_0 is the regression constant, which represents the mean intergenerational change in adult body weight. This could be induced by environmental effects, if a time-trend in environmental effects exists that is common to all stocks. T_t is the difference in environmental effects between year t and year $t - 2$ common to all stocks in the experiment. T_t represents a common trend in a given 2-yr span whereas B_0 represents a common constant trend over the entire time span of the experiment. h^2 is the mean heritability of growth rate averaged over time and across stocks i . $D_{i,t-2}$ is the selection differential from size-selective fishing for stock i in year $t - 2$. This equals the mean body weight of the parental generation just after selective fishing minus that just prior to selective fishing (Falconer 1989). $E_{i,t}$ is the residual effect, unique to stock i , of the difference in adult body weight between year t and year $t - 2$.

The assumptions of this statistical model are that $E_{i,t}$ are independent and identically distributed and $D_{i,t-2}$ are uncorrelated with $W_{i,t-2}$. See the section on estimation of parameters for comments on these assumptions.

Experimental Design

Experimental designs were developed to test at $\alpha = 0.05$ the null hypothesis that h^2 in equation (1) was 0 when the simulated true value was between 0.18 and 0.25 (see below). Spatial replicates should be statistically independent insofar as treatments in one replicate should not affect responses in others (Hurlbert 1984). We therefore suggest terminal fisheries as the units for spatial replicates in order to reduce interception of fish migrating to nonlocal fisheries. Spatial replicates should in theory also contain single breeding populations of pink salmon to ensure intrastock as opposed to interstock selection (Nelson and Soule 1987). Some stocks would be selectively fished by gillnet gear. Others would be nonselectively fished by seine gear. Troll gear accounts for less than 5% of the annual catch biomass in the statistical areas proposed for experimentation and could be excluded to simplify implementation. Selection differential would be measured in each area and year by sampling mean adult body size with seine nets just prior to and just after fishing. In each spatial replicate, selective gear would be alternated yearly with nonselective gear to control for area-specific effects (Hurlbert 1984).

The simplest form of a controlled, replicated design (i.e. a block design, Fig. 2) would initiate treatments in the same year in all spatial replicates. Spatial and temporal replication and control areas without size-selective fishing should prevent confounding of environmental effects on body size (i.e. B_0 and T_t in equation (1) above) with genetic effects of size-selective fishing. Therefore, the proposed designs should facilitate unbiased estimation of h^2 . Logistical details of this design and its feasibility are discussed further in McAllister (1990).

McAllister (1990) also examined the staircase design, where treatment begins sequentially in different spatial areas so that artificially and environmentally induced trends in estimated parameters can be statistically distinguished (Walters et al. 1988, 1989). However, we do not discuss this here because McAllister (1990) found that the block design performed at least

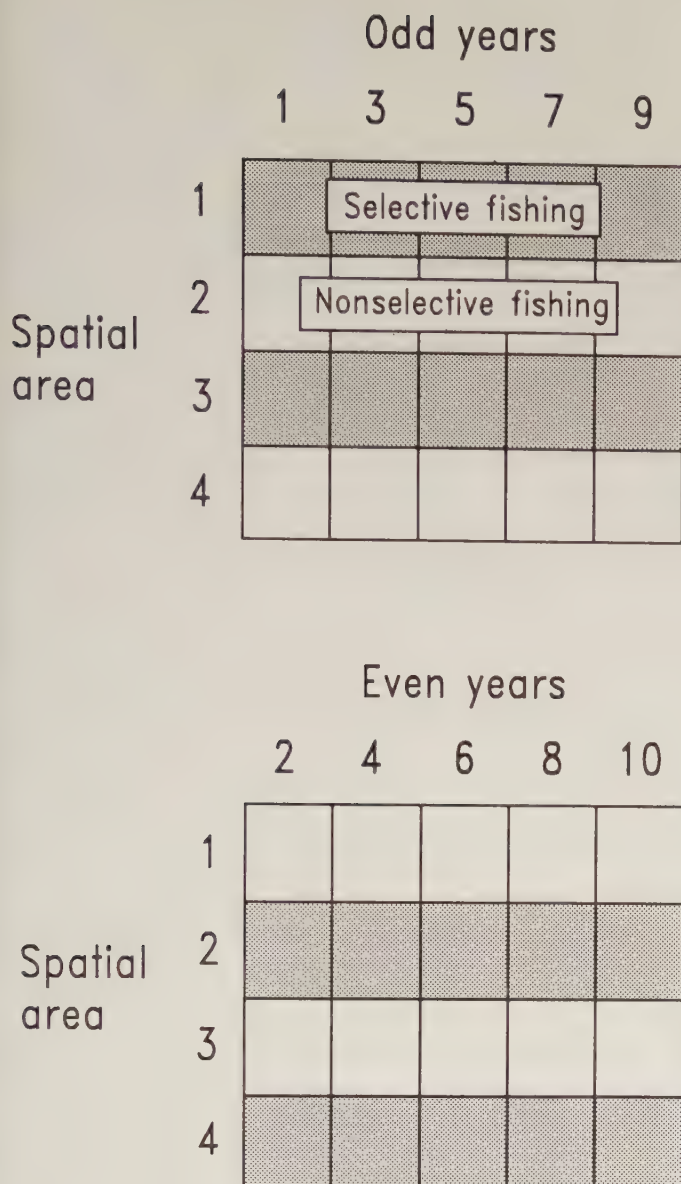


FIG. 2. Diagram of a block experimental design. This design has a duration of 10 yr and four spatial areas containing both even- and odd-year stocks of pink salmon. Selective and nonselective fishing are initiated in years 1 and 2 (reprinted with permission from McAllister and Peterman 1992a).

as well as the staircase design in our pink salmon situation. This was largely because of the staggered times of initiating treatments in the staircase design, which required the staircase experiment to be run for longer than the comparable block design in order to yield as high power or as low SE estimates.

Power Analysis by Empirically Based Monte Carlo Simulation

In order to compute power, possible sets of results in each alternative experimental design were simulated 500 times with random variation. Most of the parameters and variances used to simulate mean adult body weight were estimated beforehand from regressions of historical catch data using equation (1) (see below). In each individual simulation of an experiment, we tested the null hypothesis that $h^2 = 0$ and computed P , the probability that the estimate for h^2 could have resulted by chance

alone from populations with a true mean $h^2 = 0$. Power was computed as the proportion of times out of all the simulations for a given design that the computed P value was less than α (i.e. 0.05); this was because the null hypothesis (i.e. $h^2 = 0$) was false in all simulated cases. See Fig. 3 for a flowchart of the Monte Carlo procedure.

Estimation of parameters

Several parameters were needed for each simulation: (1) the initial mean adult body weight of each stock in the experiment, (2) h^2 , (3) the variance in the random effects on adult weight unique to each stock in each generation, (4) the variance in random effects common to all stocks in each generation, (5) the mean selection differential, and (6) the interannual variance in selection differential. General procedures for estimating these parameters are given below; details are described in McAllister (1990).

In our analyses, we should ideally use data from terminal fishery areas which could serve as spatial replicates in the experiment, but such data are not available. Instead, we used data amalgamated for entire statistical areas which contain several terminal fisheries (Fig. 4). Further comments on this approach are made in the Discussion.

The source of estimates of the initial weights simulated in each year is as follows. Mean adult body weights of pink salmon in 1987 and 1988 were for B.C. statistical areas 2W, 3, 4, 5, 6, 7, and 8 for even years and the same excluding 2W for odd years (Fig. 4). Mean weights were calculated by dividing the total weight of the purse-seine catch by the total number of pink salmon caught by seine in each of the statistical areas. Data were obtained from M. Henderson (Canada Department of Fisheries and Oceans (DFO), 555 W. Hastings St., Vancouver, B.C.).

We estimated h^2 using historical data and equation (1). Historical catch data (by gear type in pieces and weight) and escapement data for statistical areas 4, 5, 6, 7, and 8 for years 1965–88 (Fig. 4) (data provided by M. Henderson, DFO, Vancouver, B.C., and T. Beacham, Pacific Biological Station, Nanaimo, B.C., respectively) were used to estimate $W_{i,t}$, $W_{i,t-2}$, and $D_{i,t-2}$ in equation (1). The constant B_0 was removed from equation (1) because B_0 was nonsignificant in the regressions described below (e.g. for areas 7 and 8 from years 1965–86, $B_0 = 0.00076$, $P > 0.9$, $N = 40$). Furthermore, $D_{i,t-2}$ and $W_{i,t-2}$ were found to be uncorrelated (e.g. for areas 7 and 8 and years 1965–85, $r = -0.106$, $P > 0.4$, $N = 42$). The residuals of $E_{i,t}$ and T_i were checked and found to be serially uncorrelated (t -test) and normally distributed (Anderson–Darling statistic from Stephens 1974) (McAllister 1990). Regressions using data from statistical areas 4, 5, and 6 yielded an estimate of h^2 of 0.25 (SE = 0.15); areas 6 and 7, 0.18 (SE = 0.11); and areas 7 and 8, 0.22 (SE = 0.10). These values of h^2 were used in the sensitivity analysis. Our estimates of h^2 closely match Ricker et al.'s (1978) minimum estimates.

We simulated two forms of random variation in mean adult weight. These were (1) effects common to all stocks in a given year (these time effects could include oceanographic and density-dependent effects on mean adult size common to all stocks in each year) (t_i , where $T_i = t_i - t_{i-2}$) and (2) effects unique to each stock in a given year (called residual effects here — these include measurement error and possibly density-dependent and oceanographic effects unique to each stock in each year) ($e_{i,t}$, where $E_{i,t} = e_{i,t} - e_{i,t-2}$). Variances in $E_{i,t}$ and T_i were estimated from regressions that used the same historical catch data used to estimate h^2 and equation (1). However, we needed estimates of the variance in $e_{i,t}$ and t_i for the simulations.

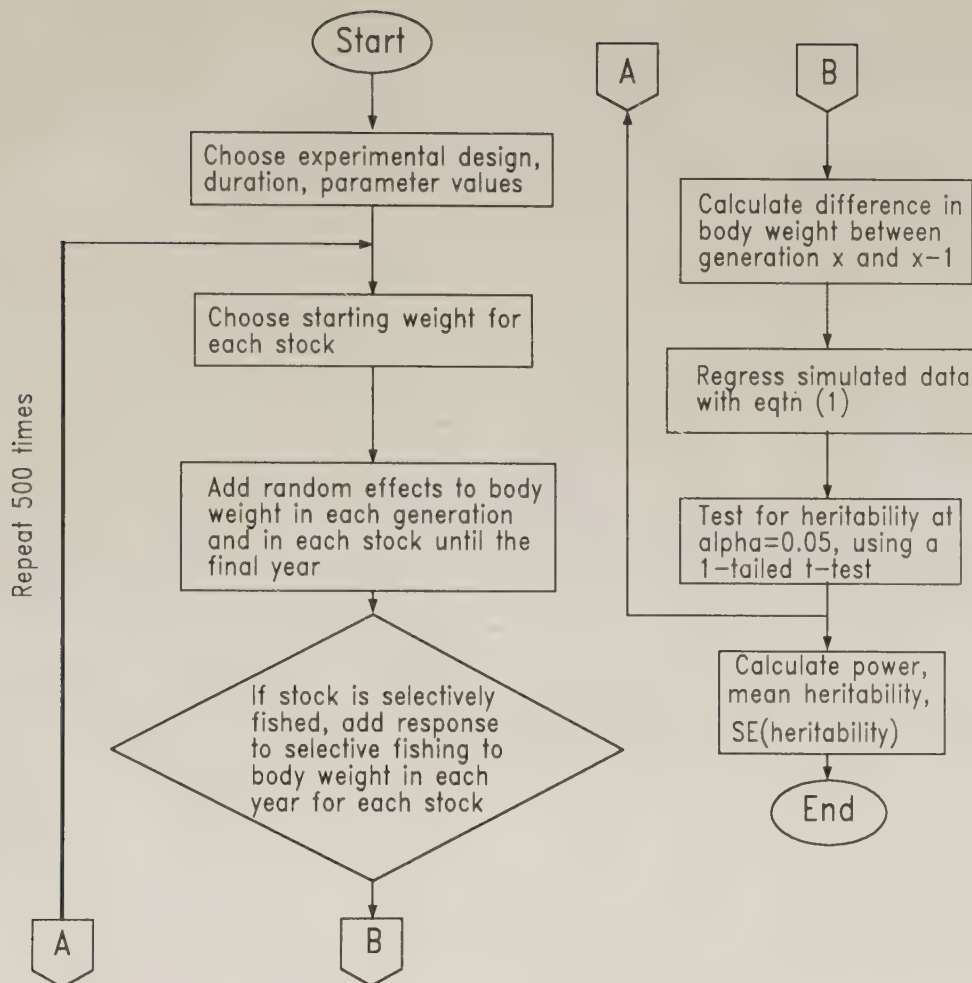


FIG. 3. Flow chart showing the basic steps in the empirically based Monte Carlo procedure that was employed to estimate the statistical power and parameter variance for alternative experimental designs.

In order to estimate the variance in t_i and $e_{i,t}$, we divided the variance estimates for $E_{i,t}$ and T_i by 2. This step follows from (1) the principle of additivity of variances for uncorrelated variables (e.g. $\text{var}(T_i) = \text{var}(t_i) + \text{var}(t_{i-2})$) and (2) the expectation that $\text{var}(t_i) = \text{var}(t_{i-2})$ and $\text{var}(e_{i,t}) = \text{var}(e_{i,t-2})$. Thus, for example, $\text{var}(T_i) = 2\text{var}(t_i)$ and $\text{var}(T_i) = \text{var}(T_i)/2$.

We defined the baseline estimates of variance in residual effects as the minimum estimates given by regressions that used pairs of adjacent statistical areas. We used data from adjacent areas because this gave smaller variance in residuals than data from pairs of nonadjacent areas. Fish from adjacent areas share more environmental conditions than ones in nonadjacent areas. Terminal fisheries in the pair that yielded the smallest estimate of residual variance could potentially yield the highest power test and therefore could be the best candidates for experimentation. The baseline SD of $e_{i,t}$ was thus 0.046 kg from areas 7 and 8, and the SD of t_i was 0.265 kg. In the sensitivity analyses, we used high and low values for SD of $e_{i,t} = 0.059$ (using data from areas 6, 7, and 8) and 0.033 kg ($\sqrt{0.5}$ SD for areas 7 and 8). Thus, this range of variances should encompass that encountered under experimental conditions.

We used a mean selection differential (over stocks and years) of 0.25 kg in the Monte Carlo simulations (from McAllister 1990). This value was based on (1) a mean exploitation rate of 50%, which approximates the optimal exploitation rates for central B.C. coast stocks (Beacham 1984), and (2) the expected

difference in mean adult weight between gillnet- and seine-caught fish when exploitation rate was 50% and when 90% of the total catch of a stock was caught by gill net and 10% by seine gear. The estimate of interannual variance in selection differentials within each stock i (SD of $D_{i,t-2}$) of 0.057 kg was obtained from McAllister (1990).

Monte Carlo procedure (Fig. 3)

Each simulation of an experiment was initiated by choosing a mean adult weight randomly without replacement from the historically observed set of six odd-year or seven even-year adult weights, depending on whether the initial year for the replicate was odd- or even-numbered (see section on initial weights). The same set of initial body weights was used in each simulated experiment. A chance variation term ($e_{i,t}$) was randomly chosen from a normal distribution with baseline SD = 0.046 kg and mean = 0. An effect common to all stocks for this generation (t_i) was chosen randomly from a normal distribution with SD = 0.265 kg and mean = 0 and added to the adult weight to obtain the weight for stock i in that initial year, $W_{i,t}$. These SDs were estimated from historical data, as described above.

If the stock was selectively fished, an effect for selection differential ($d_{i,t}$) was chosen randomly from a normal distribution with SD = 0.057 kg. This term was added to the mean for the selection differential. The resulting selection differential was multiplied by the value for heritability to obtain the

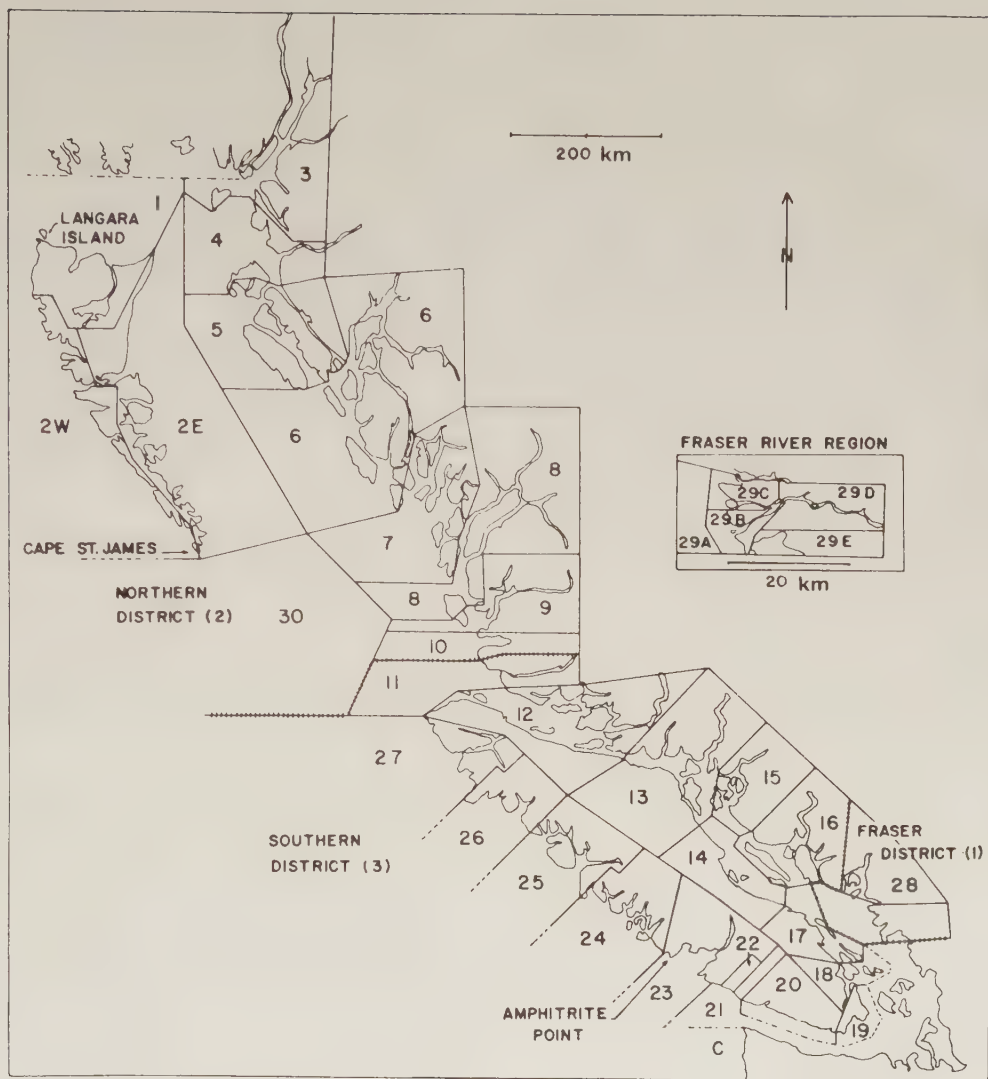


FIG. 4. Map showing the statistical areas in B.C. (reprinted with permission from Ricker 1981).

response ($R_{i,t+2}$) to selection (i.e. $R_{i,t+2} = h^2 D_{i,t}$) (Falconer 1989).

In the next simulated generation, the common time effects and stock-specific effects on weights were again drawn randomly from these respective distributions. These values and, if the stock was selectively fished, $R_{i,t}$, were added to the adult weight of the previous generation ($W_{i,t-2}$), less the common time effect (t_{t-2}) and the chance variation effect ($e_{i,t-2}$). The difference in adult weight between one generation and the next was then $W_{i,t} - W_{i,t-2}$.

The above procedure was repeated for the duration of the experiment for each spatial replicate. Next, the resulting time series of simulated data was regressed using equation (1). Using a one-tailed Student t -test, we tested the null hypothesis $h^2 = 0$ at $\alpha = 0.05$ when the true simulated value was 0.18, 0.22, or 0.25. Variance in the estimate of h^2 was estimated in each simulated experiment from the product of the residual variance and the first diagonal element of the estimated variance-covariance matrix of parameters (i.e. $\text{var}(h^2)$ = the first element in $\text{var}(e_{i,t})(X'X)^{-1}$ where X = the design matrix; X was computed from the simulated experimental data) (Draper and Smith 1981; Walters et al. 1988).

Using the above procedure, we simulated individual experiments 500 times. Power was estimated as the number of times

in which the null hypothesis was rejected, divided by 500. The mean and variance of h^2 were the means of those respective estimates computed from the 500 simulations. Baseline estimates of heritability (0.22), mean selection differential (0.25 kg), and residual variance in mean adult weight per stock (SD = 0.046 kg) were used in all simulations except where stated otherwise.

Results

We found several different designs that could be informative. In such designs, managers would have a probability >0.8 of correctly rejecting the null hypothesis that $h^2 = 0$ when it was either 0.18, 0.22, or 0.25 in nature and α was 0.05. Note that all designs led to unbiased estimates of h^2 (i.e. the mean estimates of h^2 from 500 simulations were within $\pm 5\%$ of the simulated true value for each design); hence, for the remainder of this paper we do not refer to the mean estimate of h^2 . The SE of h^2 was used to determine whether designs would yield satisfactory precision in the estimate of h^2 .

Baseline Case and Sensitivity Analyses

Baseline results are for a 10-yr experimental design with four spatial replicates. By "10-yr" we mean 10 yr of application of

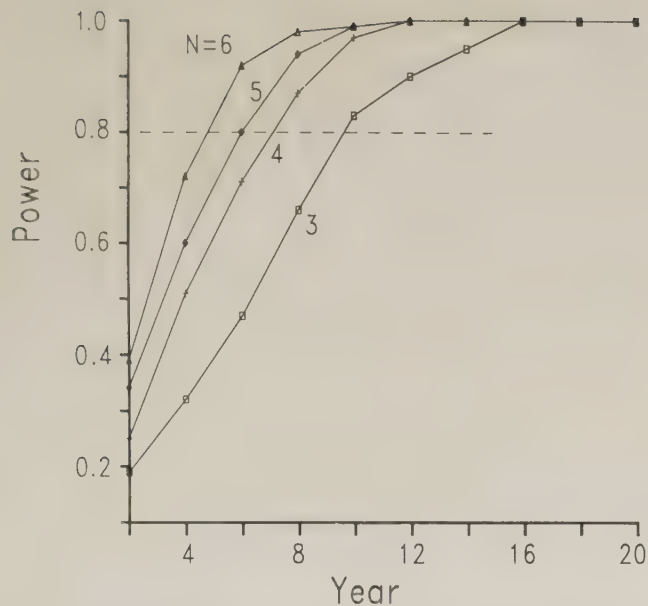


FIG. 5. Statistical power versus time for block designs with three, four, five, and six spatial replicates. Baseline parameter values were $h^2 = 0.22$, mean selection differential = 0.25 kg, and variation in residual effects (SD) = 0.046 kg.

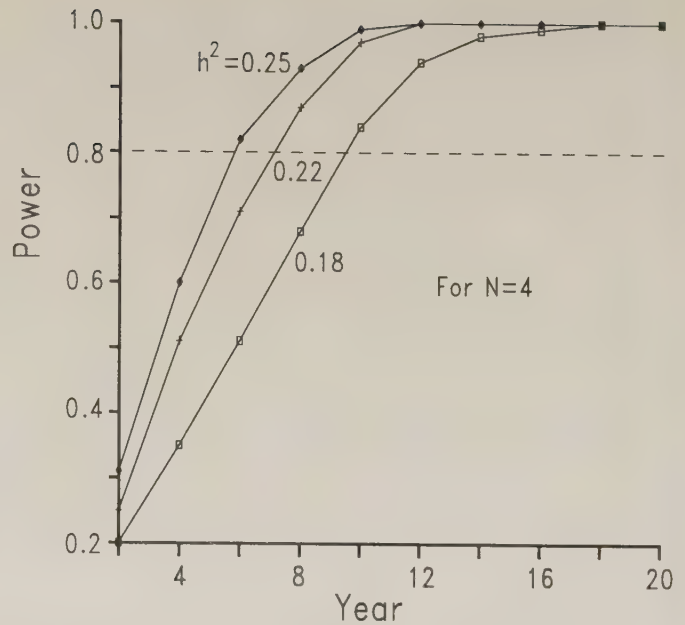


FIG. 7. Statistical power versus time for block design with $h^2 = 0.18$, 0.22, and 0.25. Baseline parameter values were four spatial replicates, mean selection differential = 0.25 kg, and variation in residual effects (SD) = 0.046 kg.

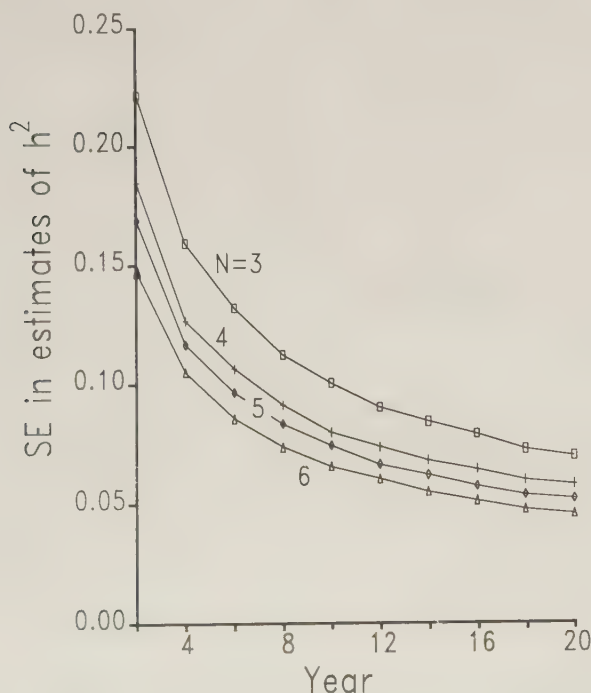


FIG. 6. Standard error versus time showing standard error curves for block designs with three, four, five, and six spatial replicates. Baseline parameter values were $h^2 = 0.22$, mean selection differential = 0.25 kg, and variation in residual effects (SD) = 0.046 kg.

selective and nonselective fishing (Fig. 2). Because of the 2-yr life cycle of pink salmon, measurements of $W_{i,t}$ would start in the second year and finish 1 yr beyond the last year of treatment. Measurements of $D_{i,t}$ would begin in the first year of treatment and end in the last. Using baseline estimates of parameters, statistical power was 0.97, i.e. a 0.97 probability of correctly rejecting the H_0 when $h^2 = 0.22$ (Fig 5). This also means that there is only a 0.03 chance of a type II error (i.e. incorrectly accepting the null hypothesis that $h^2 = 0$ if h^2 was

0.22 in the experimental populations). $SE(h^2)$ for the baseline design was 0.08 (Fig. 6). Unless stated otherwise, all sensitivity analyses below used baseline parameter values.

In the first sensitivity analysis, we varied the number of spatial replicates and experimental duration. Power exceeded 0.8 in 5–10 yr, depending on the number of spatial replicates (Fig. 5). With only three spatial replicates, it would take 10 yr for power to exceed 0.8; with six spatial replicates, it would take 5 yr.

SE of h^2 in the first sensitivity analysis decreased with increasing number of spatial replicates and duration of experiment (Fig. 6). Thus, if precision is not sufficient when power = 0.8, precision could be increased to desirable levels by increasing temporal duration, the number of spatial replicates, or both. For simplicity, we report only power in the following sensitivity analyses. Designs with low SE of h^2 also had high power.

In the second sensitivity analysis, we tested the influence of the size of the effect (i.e. the simulated true h^2) on statistical power (Fig. 7). The baseline number of spatial replicates in this and all subsequent analyses was four. Power exceeded 0.8 in 6 yr at the high estimate of heritability (0.25) and in 10 yr for the low estimate (0.18). This compares with 7 yr for the baseline case where $h^2 = 0.22$.

In the third sensitivity analysis, we evaluated the effect on power of different values for mean selection differential (i.e. the difference in mean adult body weight of a single breeding population just after selective fishing minus that just before selective fishing). Power exceeded 0.8 in 4–10 yr, provided that mean selection differential was at least 0.20 kg (Fig. 8). A mean selection differential of 0.20 kg would require 10 yr for power to exceed 0.8; one of 0.35 kg would require only 4 yr. However, if mean selection differential was 0.15 kg, it would take 16 yr for power to exceed 0.8.

Fourth, we evaluated the effect on power of high and low variability in the year-to-year deviation in weight unique to each stock of pink salmon, $e_{i,t}$. This was an attempt to explore the performance of the experimental design with stocks that had

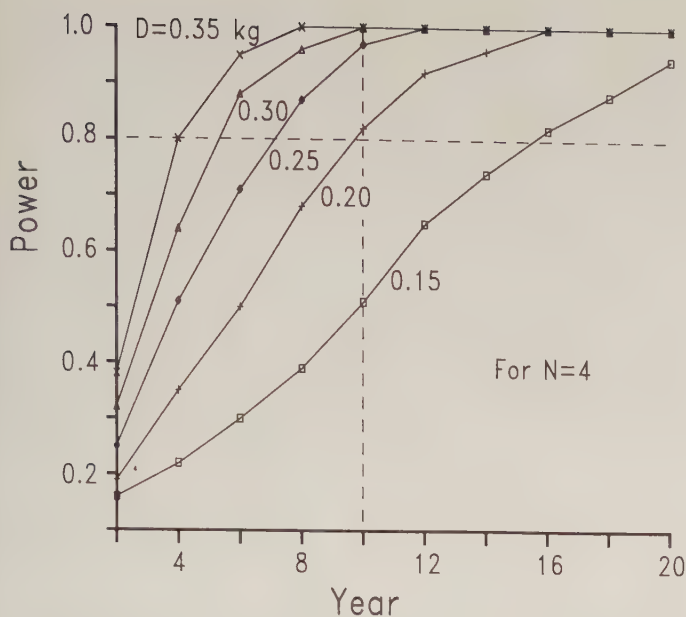


FIG. 8. Statistical power versus time for block design with mean selection differential = 0.15, 0.20, 0.25, 0.30, and 0.35 kg. Baseline parameter values were four spatial replicates, $h^2 = 0.22$, and variation in residual effects (SD) = 0.046 kg.

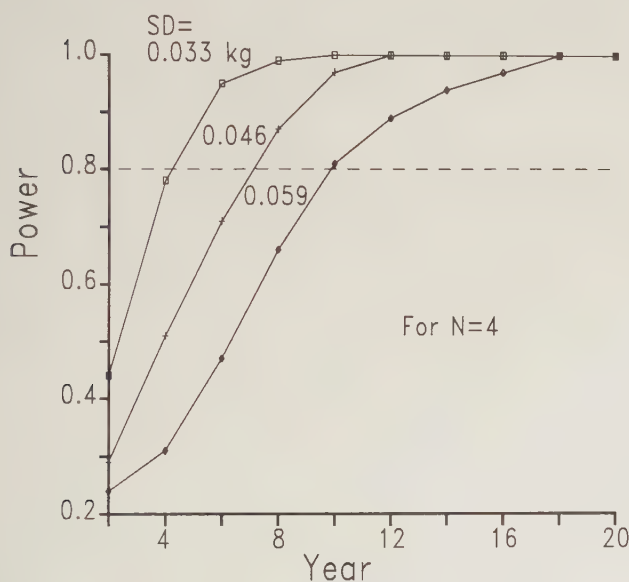


FIG. 9. Statistical power versus time for block design with SDs for random effects unique to each stock = 0.033, 0.046, and 0.059 kg. Baseline parameter values were four spatial replicates, $h^2 = 0.22$, and mean selection differential = 0.25 kg.

either higher or lower residual variation in body weight than our baseline case. Power exceeded 0.8 in 5 yr for the minimum amount of variation (SD = 0.033 kg) and in 10 yr for the maximum amount (SD = 0.059 kg; Fig. 9). Power was insensitive to different values for variance in t_i , the variance in weight common to all stocks, because the corresponding effects, T_i , were estimated and removed from the residual variance in each regression.

Discussion

Our statistical power results suggest that a large-scale fishing experiment on B.C. pink salmon is a promising method to

determine whether growth rate is sufficiently heritable to support the conclusion that size-selective fishing is an important source of change in adult body weight. Under most conditions examined, 5- to 10-yr experimental designs would yield power greater than 0.8. An experiment with only four spatial replicates and a mean selection differential of 0.25 kg would yield power of 0.87 in 8 yr, for $h^2 = 0.22$ (our current estimate of h^2). For a 10-yr experiment, power would be 0.83 if $h^2 = 0.18$, 0.97 if $h^2 = 0.22$, and 0.99 if $h^2 = 0.25$. Thus, power would be high for the range of h^2 values necessary to explain the historical decline in body weight via the size-selective fishing hypothesis. Because power would be high, there would be at most a probability of 0.17 of making a type II error for those values of h^2 . If h^2 was <0.18 , then size-selective fishing cannot account for the observed changes and lower power will not matter. Thus, regardless of the outcome of the experiment, managers would be confident in their conclusion about the relative importance of size-selective fishing. That conclusion would be relevant to design of remedial measures as well as interpretation of past decreases in body weight.

Managers could also evaluate proposed designs in terms of their SE of h^2 , given that all designs led to unbiased estimates of h^2 . If managers wanted SE to be <0.10 , all designs with power >0.80 would be satisfactory. But if managers wanted higher precision, they would have to consider designs with more spatial replicates and longer durations (see Fig. 6). SE for estimates of heritability for various characters in various animal species reported in Falconer (1989) ranges from 0.02 to 0.10.

Factors Affecting Mean Selection Differential

Several issues need to be addressed in order to make our proposed experimental design work in the field. Our sensitivity analysis indicates that mean selection differential (D) can strongly influence statistical power. For example, only values of D of 0.20 kg and greater yielded power >0.8 in less than 10 yr when there were four spatial replicates (Fig. 8).

In a field situation, selection differential can be manipulated by changing management regulations that influence different aspects of the fishery. We suggest several possibilities. First, and most importantly, smaller mesh sizes could be imposed to selectively harvest smaller sized individuals rather than the larger fish in the population as at present. Second, hang ratios (i.e. length of net webbing per net length, which is currently 3:1 in most fisheries) could be reduced to increase the size specificity of gill nets because nets with low hang ratios tangle fewer fish and thereby target a more specific size range than nets with more webbing (Wilson and Andrews 1987). Third, less supple net material could be required. For example, net materials such as monofilament that are less supple than others also tangle fewer fish (Wilson and Pearse 1984). Fourth, the timing of each terminal fishery could be adjusted so that fish could be caught at the earliest possible stage of maturity before the development of pronounced spawning morphology (e.g. sexually mature fish with hooked noses and enlarged teeth tangle more readily than less mature individuals of the same size; this reduces the size specificity of gill nets; Von Brandt 1974; Hamley 1975; Wilson and Pearse 1984). Small-scale field trials could help to develop gillnet regulations that could maintain an appropriate mean selection differential (e.g. 0.20 kg) in an experimental fishery.

Regulations that could increase the selectivity of nets for smaller fish could make the gear less efficient so that it caught fewer fish per unit effort (Riedel 1963) and fewer fish of larger sized, more valuable species such as sockeye salmon (*O. nerka*) (Wilson and Pearse 1984; Wilson and Andrews 1987). How-

ever, as noted above, nets could be made more efficient and selective for smaller than average size fish by requiring the use of monofilament nets with smaller mesh sizes than nets currently used.

Effects on Additive Genetic Variance

Size-selective fishing for several generations could have reduced additive genetic variation in growth rate and heritability of growth rate, and could thereby limit possible responses in mean adult body size to the size-selective fishing proposed as part of our experiment. However, Ricker et al. (1978) suggested that at the historical levels of selection in B.C. pink salmon, "it may take considerably longer than 25 generations" before existing genetic variation in growth rate was completely depleted. The point at which there are no further phenotypic responses to directional selection is termed the "selection limit" (Falconer 1989). The rate at which the selection limit is reached is positively related to the intensity of selection (i) and inversely related to the number of loci contributing to variation in the selected trait and effective breeding population size in each generation, where i = the selection differential divided by the SD in total phenotypic variation in the selected trait (Falconer 1989). In some experimental studies, the selection limit has been reached in 20–30 generations (e.g. Falconer 1955; Clayton and Robertson 1957). In these studies, phenotypes at the very extremes have been bred to achieve strong directional selection, and mean values of i were high (e.g. 1.1 in Falconer (1953) and 1.4 in Clayton and Robertson 1957)). Effective breeding populations in most of these studies have ranged between 15 and 32 individuals (Falconer 1989). However, in Yoo (1980), where the effective breeding population was 60 individuals and i was 1.4, the selection limit was approached in 75–89 generations.

In the proposed experiment and in the past, selection intensity from size-selective fishing on B.C. pink salmon has been considerably less than in the above studies on selection limit. The SDs in phenotypic variance in mean adult weight for even- and odd-year B.C. pink salmon are 0.46 and 0.55 kg, respectively (Ricker et al. 1978). With a selection differential of 0.25 kg, selection intensity, i , would be 0.5 for even-year fish and 0.6 for odd-year fish. Historical values for i since the 1950s for odd- and even-year B.C. pink salmon are 0.2 and 0.3, respectively (Ricker et al. 1978). Because the intensity of selection has been smaller and effective breeding population size is larger in wild populations of pink salmon than for animals in laboratory experiments, it is unlikely that the selection limit has been reached or would be approached in the proposed 10- to 20-yr experiment.

Other Factors Affecting Statistical Performance

It is unclear whether new fishing regulations could maintain consistently strong directional selection to induce a satisfactory increase in mean adult body weight. As well, straying of adult pink salmon from natal streams, especially between areas with contrasting treatments, could also decrease power. Actual selection differentials in selectively fished areas could be reduced by straying between selectively and nonselectively fished areas after size-selective fishing takes place. In that case, the $D_{i,t-2}$ estimated from the field data taken immediately before and after fishing would be higher than the selection differential actually realized in the population. In addition, straying between areas with contrasting treatments both before and after selective fishing would tend to create more similar mean

weights in those areas. Thus, the response to selection estimated from field data ($W_{i,t} - W_{i,t-2}$) would be less than the actual response that would occur in the absence of straying. Such biases in measurements of variables could result in a biased estimate of h^2 , increased residual variance, and reduced power. Thus, it is important that managers choose replicate areas to reduce effects of straying on the statistical performance of the experiment.

Frequency-dependent selection on body size during spawning (i.e. selection on body size that results from the relative frequency of different sizes of competing individuals in the spawning population) (Gross 1985) could also lead to a different statistical power in the field than we calculate here. This is because a high density of large female spawners relative to that of smaller ones, for example, could generate lower reproductive success of spawners than we assume with a concomitant reduction in the rate of increase in mean adult size over time.

In contrast with the above cases, there are a number of factors that could potentially lead to higher power in the field than expected from our baseline simulations. For example, the baseline estimate of residual variance that we used in our simulations could be larger than that obtained in a field experiment. The accuracy of our empirical estimates of mean adult weight just prior to fishing ($W_{i,t}$) and selection differential ($D_{i,t}$), upon which our estimates of residual variance are based, is affected by inaccuracies and imprecision in estimates of escapement, spatial distribution of the catch by different gear types, non-catch mortalities, straying, and interception rates of pink salmon in other statistical areas. More accurate and precise estimates of $D_{i,t}$ and $W_{i,t}$ than those used in the current analysis could be produced by (1) careful choice of replicates such that they reduce straying of adult pink salmon among replicates and (2) sampling for mean adult weight just before and just after experimental fishing in each year on each stock. These steps could reduce residual variance and increase statistical power and precision in the estimate of h^2 .

Our estimates of residual variance could also be larger than those obtained in an experiment if the experiment took place among stocks in one rather than two statistical areas (from which baseline variances were estimated for the simulation). Residual variance tends to increase as the geographic range among spatial replicates increases because as the range increases, fewer spatial and temporal locations are shared by stocks (Walters et al. 1988, 1989). For instance, variance in $e_{i,t}$ was larger when equation (1) was regressed with data from statistical areas 6, 7, and 8 (SD = 0.059 kg) than with just areas 7 and 8 (SD = 0.046 kg) (McAllister 1990).

Comparisons with Other Experimental Harvest Examples

Compared with most other proposed large-scale fishing experiments, this analysis suggests that a relatively short duration experiment can achieve high power. Allen and Kirkwood (1976) reported that with a 20% coefficient of variation (CV) in an index of abundance of a whale population, it would take 13 yr for managers to be able to detect with 0.88 probability a 5% decrease in abundance per year. Furthermore, after 13 yr, abundance would be reduced to 54% of the original amount. The authors concluded that such a result would be unacceptable. For an experiment currently under way that tests hypotheses on the effects of different fishing techniques on demersal fish production, Sainsbury (1988) reported that learning periods longer than 12 yr would be required for good model discrimination. Walters and Collie (1989) reported the results of an evaluation of a proposed experiment that is designed to

determine the exploitable stock size of B.C. Pacific ocean perch (*Sebastes alutus*), which do not recruit until ages 8–12. It would take 20–30 yr to detect the effects of unrestrained fishing on recruitment if no stock collapse occurred.

In contrast with stock abundance, which is the focus of most large-scale fishing experiments (Allen and Kirkwood 1976; Tyler et al. 1982; Sainsbury 1988; Walters and Collie 1989; Collie et al. 1990), mean adult body weight of pink salmon — the response variable in the current experiment — can be measured relatively precisely. For example, the CV in mean weight is roughly 1% using a sample size of 1000 and a single stock of odd-year pink salmon (SD in weight within odd-year populations = 0.55 kg; from Ricker et al. 1978). This compares with a CV in the index of whale abundance of 20% in Allen and Kirkwood (1976). Thus, providing that sample size was large enough (e.g. >1000 fish) and straying rates of adult pink salmon were small (e.g. <5%), measurement or estimation error would not be a problem for the current proposed experiment, as it may be for others.

Generally, the results in the current analysis are more optimistic than for other situations with fewer spatial replicates, biological variables that are more difficult to measure, and species that are longer lived and have more complicated life histories. The uniform 2-yr age at maturity, large number of separate pink salmon breeding populations on the B.C. coast, and their semelparous and anadromous characteristics facilitate temporal and spatial replication and experimental manipulation. Thus the current proposed experiment on B.C. pink salmon offers more opportunity for learning than is typical for large-scale fishing experiments.

Management Implications

As noted above, there are some practical difficulties for implementation such as finding at least three suitable spatial replicates and developing appropriate gear regulations for them. The practicality of a large-scale experiment can be further assessed by a more detailed study of the terminal fisheries for pink salmon stocks and by small-scale experiments with different types of gill nets to assess their size selectivity for smaller than average size pink salmon. The results of our sensitivity analyses provide general guidelines for developing the proposed experimental harvest strategy.

Although some of the experimental designs examined above were potentially informative, managers probably need to be convinced that an experiment would yield economic benefits over the current management approach before they might seriously consider an experiment. The potential economic benefits of our proposed experimental harvest strategy for B.C. pink salmon are evaluated using formal decision analysis in McAllister and Peterman (1992b).

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Decision Analysis of a Large-Scale Fishing Experiment Designed to Test for a Genetic Effect of Size-Selective Fishing on British Columbia Pink Salmon (*Oncorhynchus gorbuscha*)

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Past work suggested that size-selective harvesting of large fish combined with heritability of body size has caused the large (up to 34%) decrease in mean adult weight of British Columbia pink salmon (*Oncorhynchus gorbuscha*) since 1950. In a companion paper (Can. J. Fish. Aquat. Sci. 49: 1294–1304) we evaluated the statistical performance of a large-scale fishing experiment that could enable managers to test this hypothesis and at the same time increase catch biomass if that hypothesis were correct. In this paper we evaluate the economic performance of the proposed experiment using Monte Carlo simulation and decision analysis under a wide range of conditions that encompasses existing biological uncertainties. We accounted for uncertainties through prior probabilities placed on two key biological hypotheses. We computed the expected economic value of catch biomass for the experimental and current nonexperimental (status quo) management strategies using a 20-yr time horizon and a 10-yr experiment with four spatial replicates. Under a variety of discount rates, the expected economic value of experimentation exceeded that of status quo management in most of the conditions examined, in some cases by as much as 60%.

Certains travaux antérieurs portent à croire que la pêche sélective visant les gros poissons combinée à l'hérabilité de taille soit à l'origine de l'importante baisse (jusqu'à 34 %) du poids moyen des adultes du saumon rose (*Oncorhynchus gorbuscha*) de la Colombie-Britannique notée depuis 1950. Dans une communication annexe (J. can. sci. halieut. aquat. 49 : 1294–1304) nous avons évalué le rendement statistique d'une expérience de pêche à grande échelle qui devrait permettre aux gestionnaires de tester cette hypothèse et, par la même occasion, d'accroître la biomasse des prises si l'hypothèse s'avère juste. Nous avons évalué le rendement économique de l'expérience proposée en faisant appel à la simulation Monte Carlo et à l'analyse décisionnelle dans une large gamme de conditions qui recouvrent les incertitudes biologiques actuelles. Nous avons tenu compte des incertitudes en assignant des probabilités à deux hypothèses biologiques clés. Nous avons ensuite calculé la valeur économique prévue de la biomasse des prises en stratégies de gestion expérimentale et non expérimentale (statu quo actuel) au cours d'une période de 20 ans et d'une période expérimentale de 10 ans en répétant les essais en quatre lieux. Dans la plupart des conditions examinées et pour divers taux actualisés, l'expérience a permis d'obtenir une valeur économique supérieure, dépassant dans certains cas de 60 % celle de la gestion non modifiée (statu quo).

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Experimental approaches to management have been advocated in several fisheries management situations (Larkin 1972; Walters and Hilborn 1976, 1978; Holt 1977; Tyler et al. 1982; Sainsbury 1988; Walters et al. 1988, 1989; Walters and Collie 1989; McAllister and Peterman 1992; McAllister et al. 1992). In all of these cases, authors have claimed that deliberate experimentation will help to resolve uncertainties about the underlying dynamic components of the fish populations, with subsequent improvement in their management. However, only a few proposals have been implemented (e.g. Sainsbury 1988). A major barrier to implementing experimental management is that managers need to be convinced a priori that an experimental approach has good potential to yield the desired information and to produce higher economic value than

nonexperimental management alternatives (Sainsbury 1988; McAllister et al. 1992).

However, forecasting the potential economic yield of alternative management strategies is complicated by the uncertainty in our understanding of managed systems. For example, lack of precision and accuracy in stock assessment methods makes it difficult to (1) learn about the mechanisms influencing the historical and current behaviour of managed stocks and (2) forecast possible future responses to different management strategies. Furthermore, continuing changes in fishing technology within fisheries can make it difficult to make assumptions about the future behaviour of fishermen.

Thus, when fisheries managers become interested in experimental approaches to management, they are inevitably faced with uncertainty about future costs and benefits of the alternative courses of action that they could take, including remaining with the current management practice. When faced with this uncertainty, managers have usually opted for the status quo. In doing so, they may have avoided more informative alter-

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natives that trade off short-term inconveniences against potentially large long-term payoffs to fishermen and society as a whole (Larkin 1972; Walters 1977; Silvert 1978; Clark 1985; Walters and Collie 1989).

Uncertainty about future benefits can be dealt with systematically by applying the quantitative methods of decision analysis, which (1) reduce the arbitrariness in decision-making, (2) incorporate risk and uncertainty into the evaluation of decision alternatives, and (3) maximize the probability of choosing the most beneficial option (Raiffa 1968; DeGroot 1970; Keeney and Raiffa 1976; Clark 1985; Lindley 1985; Walters 1986). Several authors have applied these decision analysis methods to fisheries management problems (e.g. Walters 1977; Sainsbury 1988; Parma and Deriso 1990).

Our purpose here is to apply decision analysis to the choice between experimental and nonexperimental approaches to solving the problem of the 34% decrease in mean adult body weight in British Columbia (B.C.) pink salmon (*Oncorhynchus gorbuscha*) since 1950 (Ricker et al. 1978). The present analysis compares the expected economic value (i.e. discounted present value) of these two management approaches under a variety of conditions. The economic results reported in this paper, together with simulated results on the statistical performance of the experimental strategy reported in the companion paper (McAllister et al. 1992), provide managers with a rational basis for evaluating whether an experimental approach to pink salmon management is appropriate.

Background

Concerns have been expressed over the large decrease since 1950 in mean adult body weight of pink salmon in B.C. (Ricker et al. 1978; Healey 1986; fig. 1 of McAllister et al. 1992). Decreased mean body size leads to decreases in potential biomass yield and value of the catch because, for a given number of fish caught, catch biomass decreases linearly with decreases in mean adult weight. Furthermore, accumulating evidence suggests that reproductive potential in salmonids may be strongly affected by parental body size, especially in females. For example, when compared with larger individuals, smaller salmon have lower survival on upstream migration (Ricker 1989), and smaller females produce fewer and smaller eggs (Foerster and Pritchard 1941), choose poorer quality nest sites, dig shallower nests, and defend their nests for shorter durations (van den Berghe and Gross 1989). They also produce smaller alevins and fry (Beacham et al. 1985), which have lower growth and survival rates (Bagenal 1969; Kobayashi 1980; West and Larkin 1987). Thus, the past decreases in mean adult body size could also have reduced the reproductive potential of B.C. pink salmon.

It is important for the future management of these and other salmon fisheries to determine the cause of the temporal decrease in pink salmon body weight. If size-selective fishing combined with heritability of body size is indeed the cause, then changes in selectivity of fishing gear may stop or even reverse the decline. However, if heritability of body size is small and past changes in body weight have been caused by oceanographic conditions or changes in abundance, then such changes in gear will not necessarily help. In this paper and its companion (McAllister et al. 1992), we therefore explored several possible designs of a management experiment devised to simultaneously yield economic value as well as information about the correct causal mechanism.

A Proposed Experimental Approach

McAllister et al. (1992) described an experimental harvest design that could provide data to test the gear selectivity hypothesis. All experimental designs that we investigated permitted the escapement of larger than average size pink salmon from the fishery (rather than the current situation where smaller sized fish have a greater chance of surviving the fishery). This design would enable managers to simultaneously test for effects of size-selective fishing on pink salmon and to increase mean body size and annual catch biomass if such effects are found to exist. McAllister et al. (1992) showed that such an experiment would provide an unbiased and relatively precise estimate of heritability, h^2 (i.e. $SE(h^2) < 0.1$), and could thereby determine whether there is potential for recovery (i.e. an increase in mean body size) under the type of size-selective fishing that we propose. By this means, experimentation could provide indirect information about the cause of the historical change in body weight.

However, in part because the cause of decreased body weight is uncertain, it is not clear whether such an experiment could yield larger economic benefits than the current size-selective fishing strategy. We refer to this current strategy as the status quo or nonexperimental approach; it selectively harvests larger than average size fish. Here we evaluate whether our proposed experiment could generate greater economic benefits, as measured by discounted value of the catch biomass, than the current size-selective fishing strategy.

Methods

Experimental Approach

We used the 10-yr-long block designed experiment described by McAllister et al. (1992, fig. 2) to evaluate potential economic benefits of an experimental management strategy. In each year, selective fishing (i.e. by gill nets) was simulated in two of the four terminal fishery areas (i.e. each fishery being located adjacent to the mouth of a separate spawning stream). Size selection to remove smaller than average size fish could be achieved in practice by requiring the use of smaller mesh size monofilament gill nets than at present (Wilson and Pearce 1984; McAllister et al. 1992). Nonselective harvest (i.e. by purse seines, as a control) was simulated in two other areas. Because of the biennial life cycle of pink salmon, four spatial areas incorporated eight distinct pink salmon populations. In our simulations we assumed that there are no interactions among replicate populations.

Status Quo or Nonexperimental Approach

In simulations of the nonexperimental or status quo fishing strategy, all four spatial areas and eight pink salmon populations were fished with identical gear each year, which selectively removed the larger fish in each year's population. This reflected current fishing patterns in pink salmon on the central coast of B.C. (Henderson and Charles 1984). This was in contrast with our experimental size-selective fishing areas, in which small fish were harvested.

Decision Analysis

We used decision analysis to compute the expected present value of the two alternative management options, experimental and status quo management (Raiffa 1968; Walters 1977; Stokey

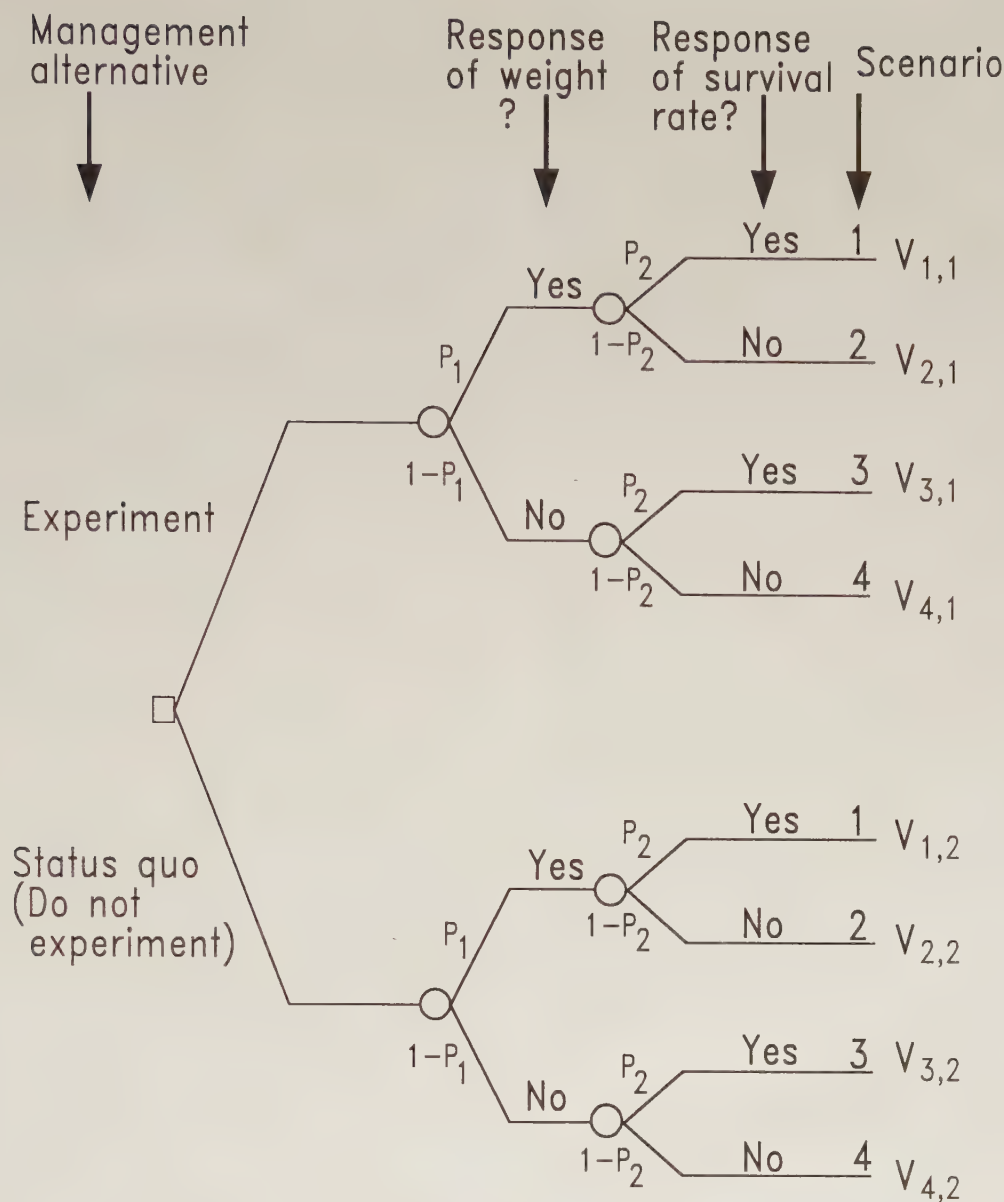


FIG. 1. Decision tree showing the two alternative management decisions that could be made in response to the problem of decreasing mean adult body weight of British Columbia pink salmon. See text for explanation.

and Zeckhauser 1978). The decision tree (Fig. 1) outlines the various uncertainties and some potential outcomes. In this figure, each of the two management options (i.e. experiment versus maintain the status quo and do not experiment) has four possible outcomes, based on two possible biological effects at each of two chance nodes. While there are many potential effects, we chose this simple scheme to cover the extreme ranges of possibilities.

Alternative outcomes

Response in mean adult weight — The first chance nodes (lefthand circles in Fig. 1) reflect the response or lack of response of mean adult weight to size-selective fishing (i.e. $h^2 = 0.22$ or $h^2 = 0$). If there was a response, mean adult body weight in subsequent generations would increase in selectively fished areas in the experiment in response to the size-selective removal of smaller sized fish (McAllister et al. 1992). However, in the case of status quo management, mean adult weight would continue to decrease in response to the current

size-selective removal of larger sized fish. If there was no response ($h^2 = 0$), mean adult weight would remain constant even if there was size-selective fishing under either experimental or status quo management. We explored other values of h^2 in the sensitivity analyses (see below).

Response in survival rate — The righthand chance nodes (Fig. 1) reflect two other possible effects of the modification of the mean body size of spawners. First, egg-to-adult survival rate may vary with the mean body size of spawners in the manner delineated below through the links among female size, egg size, fry size, and survival rates at those stages (Foerster and Pritchard 1941; Bagenal 1969; Skud 1973; Kobayashi 1980; Beacham et al. 1985; West and Larkin 1987; Ricker 1989; van den Berghe and Gross 1989). Thus, egg-to-adult survival rate may respond positively to size-selective fishing. The alternative possibility that we explore is that egg-to-adult survival rate is independent of the mean body size of spawners and therefore cannot respond to size-selective fishing.

Resulting scenarios under each management alternative

The two potential effects at each of the two chance nodes result in four discrete scenarios for each management alternative: (1) there is an evolutionary response in mean adult body weight and a response in survival rate to size-selective fishing, (2) there is only an evolutionary response in body size, (3) there is only a response in survival rate, or (4) there are no responses. Using the stochastic simulation method described below, we calculated the mean economic value, $V_{1,1}$ to $V_{4,1}$ and $V_{1,2}$ to $V_{4,2}$ (in terms of the mean present value of catch biomass), of these four scenarios for each of the two management alternatives. The above values represent the present values for the four possible scenarios for experimentation and no experimentation, respectively. We took the mean of a stochastically generated distribution of outcomes and thereby estimated "expected" values of catches.

Prior probabilities

The probability values (P_1 and P_2) at each chance node reflect the subjective probabilities that managers would place on each of the alternative biological effects prior to making a decision and taking action (Fig. 1) (Raiffa 1968; Walters 1977; Stokey and Zeckhauser 1978). P_1 represents the anticipated probability that there will be an evolutionary response in mean adult body weight to size-selective fishing. P_2 represents the anticipated probability that there will be a response of egg-to-adult survival rate to changes in size of female spawners arising from size-selective fishing.

Expected present values of harvests

The expected present value of harvests for each management alternative given P_1 and P_2 ($E(\text{present value} | P_1, P_2)$) was computed in the standard manner, by multiplying each mean end value (e.g. $V_{1,1}$) by the two probability values (i.e. P_1 or $1 - P_1$ and P_2 or $1 - P_2$) leading to that V 's branch. The products were then summed for each management alternative, experimentation and no experimentation (details given below).

Monte Carlo Procedure

A simple Monte Carlo simulation procedure was used to quantify the possible outcomes (Fig. 2).

Simulation of mean adult weight over time

The model simulated mean adult body weights in each stock by the standard formulation for a response to selection (Falconer 1989):

$$(1) \quad W_{i,t} = W_{i,t-2} + h^2 D_{i,t-2} + t_i + e_{i,t}$$

where $W_{i,t}$ = mean adult body weight (just prior to fishing) of stock i in year t of the simulation. Each stock i consists of either an even- or odd-year population of pink salmon that returns to spawn in a specific area and is caught in a terminal fishery. $W_{i,t-2}$ = mean adult body weight (just prior to fishing) of the parental generation of stock i in year $t-2$ of the simulation. h^2 = heritability of growth rate. Heritability is the ratio of "additive" genetic variance to total phenotypic variance for a particular trait in a population (Falconer 1989). Mean heritability was assumed to be constant over time and across all stocks. $D_{i,t-2}$ = selection differential from size-selective fishing for stock i in year $t-2$. This equals the mean body weight of the parental generation just after selective fishing, minus that just prior to selective fishing (Falconer 1989). t_i = the environmental effect on body weight in year t common to all stocks in the experiment. This could arise from widespread changes in availability of food in the ocean, for instance. $e_{i,t}$ = the

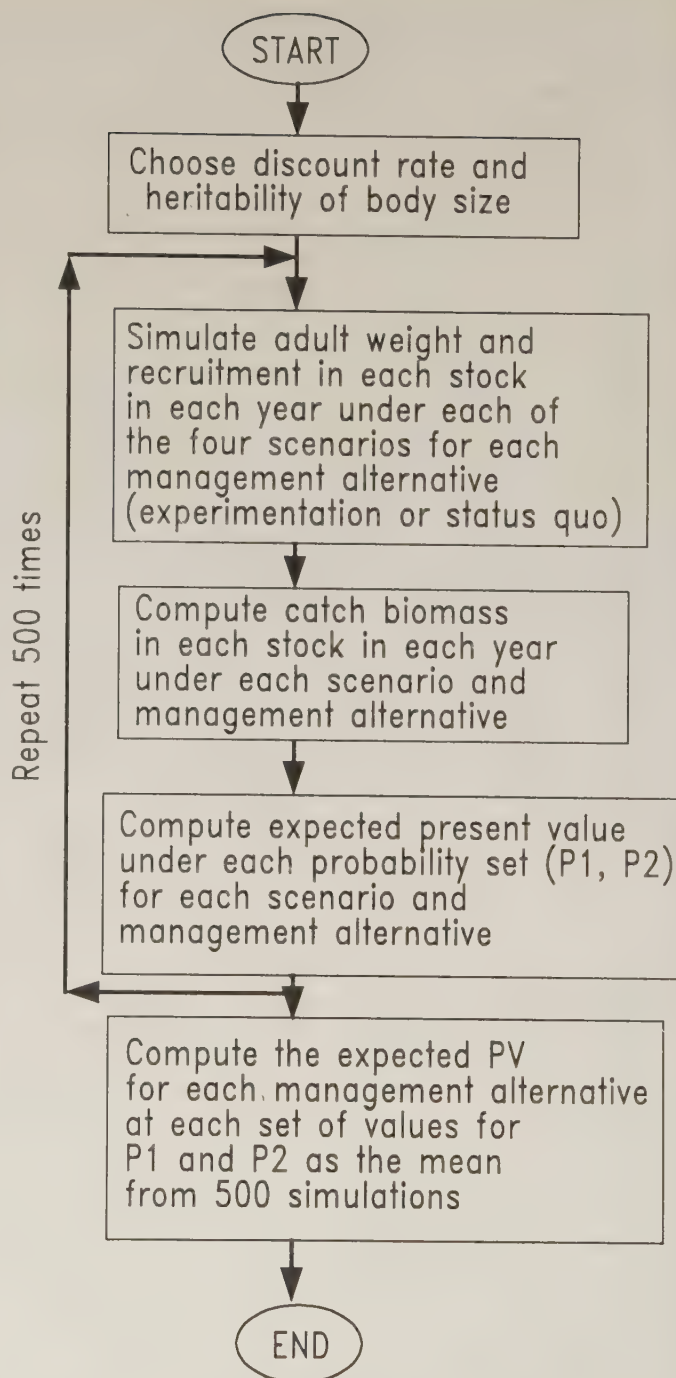


FIG. 2. Flow chart showing the basic steps in the Monte Carlo procedure that was employed to estimate the expected economic value of experimental and nonexperimental (status quo) approaches to the problem of decreasing mean adult weight.

residual effect unique to stock i in year t . t_{i-2} and $e_{i,t-2}$ were subtracted from $W_{i,t}$ just after $W_{i,t}$ was computed. Therefore, t_i and $e_{i,t}$ were independent in each year and their effects were not cumulative.

We used the same least squares estimates of parameters as in the baseline case of McAllister et al. (1992). Specifically, the baseline h^2 was assumed to be 0.22. The empirically estimated mean selection differential (D) was 0.25 kg in the experimental option. But in the status quo case, D estimated empirically was -0.18 kg for even-year and -0.05 kg for odd-year terminal fisheries. These latter estimates were based on the assumptions that 50% of the catch was caught by gill

net and 50% by seine gear (McAllister et al. 1992) and that the exploitation rates approximated the optimal ones derived by Beacham (1984) of 43% for odd-year and 69% for even-year stocks in central B.C. (i.e. statistical areas 6–10). Variances were $SD(D_{i,t}) = 0.057$ kg, $SD(t_i) = 0.265$ kg, and $SD(e_{i,t}) = 0.046$ kg.

In the simulations, mean adult body weights before fishing were computed in each stock and each year for both management alternatives. This was done using the same procedure as in the baseline case of McAllister et al. (1992). To begin each simulation of experimental and status quo options, we employed the same initial mean adult body weights of 1.99 kg for odd-year stocks and 1.39 kg for even-year stocks (computed from data provided by M. Henderson, Department of Fisheries and Oceans, 555 W. Hastings St., Vancouver, B.C., on statistical area 8 in 1987 and 1988, respectively). The random components t_0 and $e_{i,0}$ were then added to these initial weights for each stock i in year 0 to produce the variation in mean adult body weight among stocks in year 0. We chose to use baseline data from statistical area 8 because it has several terminal fisheries in it that could serve as spatial replicates or different experimental units.

Simulation of catch

The model estimated catch in each year for each stock using

$$(2) \quad C_{i,t} = (R_{i,t} - S_{i,t})/q$$

where $C_{i,t}$ = the total number of pink salmon caught, $R_{i,t}$ = the number of female recruits, and $S_{i,t}$ = the number of female spawners for stock i in year t . q = the proportion of females in the recruits, which we assumed to be 0.5. The model also assumed that fishing gear catches both sexes with equal efficiency.

We assumed a fixed escapement policy and used the Ricker (1975) stock–recruit equation (4) (see below). Based on maximum sustainable yield, optimal escapement was computed separately for even- and odd-year stocks by iteration, given the a and B parameters (Ricker 1975). We used $a = 1.85$ for even years and 0.98 for odd years (estimated for central B.C. coast pink salmon in Beacham (1984)). $B = 200\,000$ for even years and 100 000 for odd years (approximated from catch and escapement data for statistical area 8 in Henderson and Charles (1984)). The resulting estimates of escapement goals were 75 000 females for even-year stocks and 70 000 females for odd-year stocks. When returns were less than the desired escapement, a 25% harvest rate was allowed. Simulations were started assuming that returns of adults were at their optimal level.

Stock–recruit equation for trials with no survival rate response

A stock–recruitment curve normally reflects production from average-sized females. We therefore incorporated the effect on egg abundance of having larger females by multiplying abundance of female spawners ($S_{i,t}$) by a factor reflecting the change in fecundity (equation (3)). Fecundity was a linear function of average weight of spawners (Foerster and Pritchard 1941). Thus, the abundance of spawners in each stock i and year t was adjusted by

$$(3) \quad S_{\text{adj}} = S_{i,t} (F_{i,t}/F'_{i,0})$$

where $F'_{i,0}$ = mean number of eggs per female at the mean adult weight before fishing ($W_{i,0}$) of stock i in year 0 and $F_{i,t}$ = mean number of eggs per female at the mean weight of stock i in year t . See McAllister (1990) for the empirical computa-

tions of these egg abundances. Below, we refer to the mean weight after fishing as $W'_{i,t}$ where $W'_{i,t} = W_{i,t} + D_{i,t}$.

When simulating no response in egg-to-adult survival rate to changes in the mean body size of spawners, we used the Ricker (1975) spawner–recruit equation (4), adjusted only for the effect of body size on fecundity (equation (3)):

$$(4) \quad R_{i,t+2} = S_{\text{adj}} \exp [a(1 - S_{\text{adj}}/B_i) + v_{i,t}]$$

where $R_{i,t+2}$ = the number of female recruits for stock i in year $t + 2$, a = a parameter of productivity, B_i = the parameter for unfished equilibrium abundance of female spawners for stock i , and $v_{i,t}$ = the random error term (normally distributed, mean = 0) with variance estimated from the residuals found after least squares fitting of the log-transformed Ricker stock–recruit equation to historical data. Estimates of $SD(v_{i,t})$ were 0.538 and 0.444 for even- and odd-year B.C. central coast stocks (from data in Beacham 1984), respectively.

In the simulations, S_{adj} calculated from equation (3) is stochastic because $F_{i,t}$ and $W'_{i,t}$ are also stochastic. Therefore, in order to compensate for the variance introduced into the stock–recruit relationship by $W'_{i,t}$, we adjusted the empirically estimated values for $SD(v_{i,t})$ downward. Adjustments were made until the mean value for $SD^2(v_{i,t})'$ was within $\pm 1\%$ of the values observed in fits to historical data. $SD^2(v_{i,t})'$ was estimated from fits of the log-transformed Ricker (1975) stock–recruit equation to 500 randomly generated data sets. To produce 20-yr data sets, we used equations (1) and (4) and the baseline values for other parameters. Spawner number in each year was generated independently. Final adjusted values for $SD(v_{i,t})$ for even- and odd-years were 0.530 and 0.440, respectively.

Stock–recruit equation for trials with a survival rate response

Taken together, previous research suggests that egg-to-adult survival rate in salmonids could be a positive nonlinear function of parental body size (Foerster and Pritchard 1941; Bagenal 1969; Skud 1973; Kobayashi 1980; Beacham et al. 1985; West and Larkin 1987; Ricker 1989; van den Berghe and Gross 1989). For example, van den Berghe and Gross (1989) estimated that female coho salmon (*O. kisutch*) of 70 cm length had a 23-fold fitness advantage (as measured to the time of fry emergence) over 40-cm-long females. This large difference resulted because large females produced more and larger eggs, chose higher quality nest sites, dug deeper nests, and defended nests longer than small females. Thus, a linear increase in parental body size could result in an exponential increase in the abundance of recruits, all else being constant.

To incorporate a potential positive relationship between egg-to-adult survival rates and mean body size of female spawners, we modified equation (4). We adjusted parameter a in equation (4) by multiplying it by the ratio of the mean weight of spawners in year t to the mean adult weight before fishing in year 0 for stock i :

$$(5) \quad a_{\text{adj}} = a (W'_{i,t}/W_{i,0})$$

Thus, the number of returning offspring per spawner (R/S) increased with increased mean body size of spawners at abundances less than parameter B_i . As in equation (4), spawner abundance in the modified Ricker equation was adjusted to reflect the change in egg production with change in average weight of spawners, but in addition the adjusted a parameter was incorporated:

$$(6) \quad R_{i,t+2} = S_{\text{adj}} \exp [a_{\text{adj}} (1 - S_{\text{adj}}/B_i) + v_{i,t}']$$

where, $v_{i,t}'$ = the modified random error term. We adjusted the empirical values for $SD(v_{i,t})$ downward to 0.490 and 0.435

for even and odd years, respectively. As noted above, this compensated for the random variation introduced into the stock-recruit relationship by $W'_{i,t}$ (and hence by a_{adj} and S_{adj}) in the simulations. See the Discussion below for a comparison of our model results with the empirical findings of van den Berghe and Gross (1989).

Present value for each management alternative

Present values were computed over a 20-yr period following initiation of either management regime. This time horizon is large enough to encompass long-term effects of the alternatives on expected economic value. Furthermore, results differ little under different time horizons. In the years after the 10-yr experiment, we simulated one of two alternative management actions, depending on the outcome of experimentation. The first management action would result from finding an evolutionary response in body weight during the first 10 yr. In this case, (1) we assumed that 50% of the catch in each terminal fishery would be caught by seines and 50% by gill nets (this approximates current practice in some terminal fisheries) and (2) mesh sizes were regulated so that gill netters now caught fish that were 0.05 kg smaller than average. The latter action would cause a gradual evolutionary increase in mean adult body weight toward historical values if fish weight did respond to selection. The second management action would result from finding no evolutionary response in body weight. In this case, at the end of the 10-yr experiment, fishing gear in experimental areas would revert back to that in nonexperimental, status quo areas (and would therefore again selectively remove large fish).

Annual catch biomass — Annual catch biomass for each fishery was computed by summing the catch biomass for each of the gear types. The catch biomass for each gear type was computed by multiplying the total number of fish caught (calculated by equation (2)) by the proportion and mean weight of fish caught by each gear type. Catch biomass ($B_{i,j,m,t}$) was computed for each permutation of stock i , each of the four outcomes j for the biological uncertainties, each of the two management alternatives m , and each year t by

$$(7) \quad B_{i,j,m,t} = [C_{i,j,m,t} G_{i,m,t} (W_{i,j,m,t} + d_{m,t})] + [C_{i,j,m,t} S_{i,m,t} W_{i,j,m,t}].$$

When $j = 1$, there was an evolutionary response in mean adult weight and a survival rate response to size-selective fishing; when $j = 2$, there was only an evolutionary response in mean weight; when $j = 3$, there was only a survival rate response; and when $j = 4$, there were no responses. $m = 1$ for experimentation and $m = 2$ for no experimentation. $C_{i,j,m,t}$ = the total number of fish caught for stock i , outcome j , etc., $G_{i,m,t}$ = the proportion of the catch caught by gill net, $S_{i,m,t}$ = the proportion caught by seine gear for stock i , $W_{i,j,m,t}$ = the mean adult weight before fishing for stock i , and $d_{m,t}$ = the mean weight of gill net caught fish minus the mean weight of fish caught by the nonselective seine gear for management alternative m in year t . $d_{m,t}$ can be used along with exploitation rate to estimate selection differential; the values that we used for $d_{m,t}$ are empirically based (McAllister 1990). Under the status quo option, $d_{2,t} = 0.31$ and 0.05 kg in even and odd years, respectively. During the experiment, $d_{1,t} = -0.27$ kg. After the experiment, $d_{1,t} = -0.05$ kg when $j = 1$ or 2 ; when $j = 3$ or 4 , $d_{1,t} = 0.31$ and 0.05 kg in even and odd years, respectively.

In the 10-yr experiment, the size-selective removal of smaller than average size fish occurred each year from year 1 through to year 10 (McAllister et al. 1992, fig. 2).

Present value — The present value of each of the four possible outcomes for each management alternative in each simulation of a single time scenario was computed as

$$(8) \quad V_{j,m} = \sum_t \sum_i [(B_{i,j,m,t} L) / (1 + r)^t]$$

for $i = 1$ to 4 and $t = 1$ to 20

where $V_{j,m}$ = the present value of outcome j and management alternative m , B = catch biomass as above, and L = the price per kilogram of landed pink salmon in 1989 dollars. L was held constant throughout the simulation at \$1.00/kg (F. Nakashima, Pacific Net and Twine, Steveston, B.C., pers. comm.). r = the annual discount rate. For the baseline case, r was set at 0.1 (10%), a value commonly used in the evaluation of public investment decisions (British Columbia Environmental Land Use Committee Secretariat 1977) and required by the federal Treasury Board in Ottawa. Sensitivity analysis was done on r as described below.

Expected present value — The expected present value of each management alternative was calculated by first summing the products of the respective $V_{j,m}$ and the two probabilities leading to each outcome (Fig. 1). The $V_{j,m}$ for each outcome was the sum of the present values of catch biomass in each of the stocks from equation (8):

$$(9) \quad V_m = P_1 [P_2 V_{1,m} + (1 - P_2) V_{2,m}] + (1 - P_1) [P_2 V_{3,m} + (1 - P_2) V_{4,m}]$$

where V_m = the expected present value of management alternative m at probabilities P_1 and P_2 . Although certain ranges of P_1 and P_2 are more likely than others, estimates will probably vary among managers. Therefore, we explored values of P_1 and P_2 ranging from 0 to 1 at intervals of 0.1 .

The expected present value of the two management options was then estimated at each probability level P_1 and P_2 as the mean V_m derived from a 500-iteration Monte Carlo simulation. We assumed that managers were risk-neutral (i.e. that utility = some constant times $V_{j,m}$). See Keeney (1977) for a review of other types of utility functions. The percent difference in present values (PV) of the two management alternatives was calculated by $100 \times (PV_{exp} - PV_{status\ quo}) / PV_{status\ quo}$.

Sensitivity analyses

To generalize our results and test their robustness to different conditions, we performed sensitivity analyses. First, the discount rate was set at 5 , 10 , or 15% . Second, we evaluated the effect of extreme high and low values for h^2 (0.32 and 0.12) on the expected economic value of each policy option.

Results

Baseline Case

Over most of the conditions examined, experimentation yielded a higher present value of catches than status quo management. Under the baseline case (annual discount rate = 10%), the experiment yielded a larger expected present value than not experimenting in 75% of the parameter space, as defined by the range of probabilities on the uncertain biological hypotheses (Fig. 3). Note that this result pertains to the specific conditions assumed in the simulation. However, when these conditions were varied, the results were similar (see below).

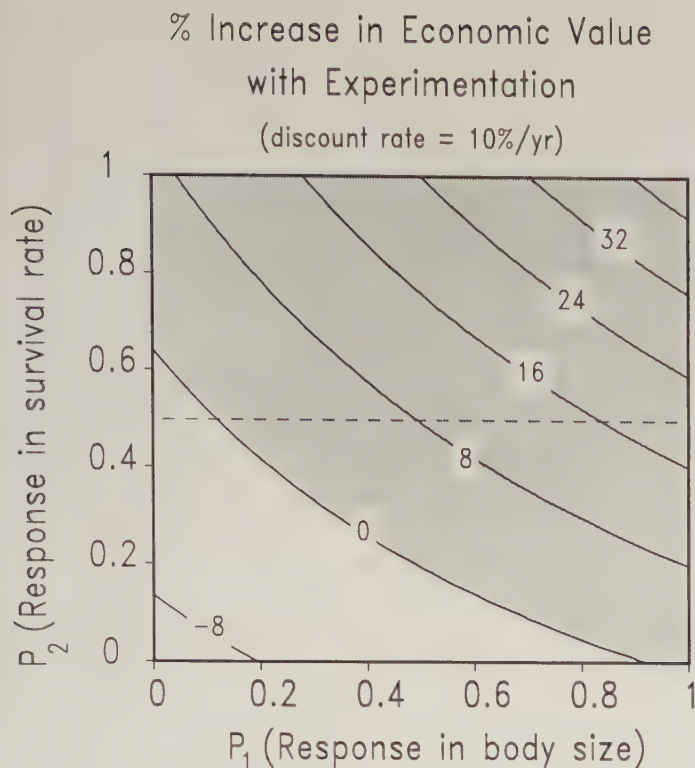


FIG. 3. Isopleths showing the percent increase in present economic value of catches resulting from experimentation compared with the value of catches from status quo management at different levels of P_1 and P_2 . P_1 = expected probability that mean adult weight will show an evolutionary response to size-selective fishing. P_2 = expected probability that egg-to-adult survival rate will vary with mean body size of spawners. Discount rate = 10%; $h^2 = 0.22$.

Most importantly, not all of the prior probabilities are equally likely. For example, prior probabilities of 0 are unreasonable for P_1 and P_2 (i.e. the anticipated probabilities for responses to size-selective fishing in body size and survival rate, respectively) given the extensive evidence suggesting genetic and survival rate responses (Foerster and Pritchard 1941; Bagenal 1969; Skud 1973; Ricker et al. 1978; Kobayashi 1980; Beacham et al. 1985; West and Larkin 1987; Ricker 1989; van den Berghe and Gross 1989). Thus, the most reasonable values for P_1 and P_2 are >0.3 , possibly in the range of at least 0.5. If a manager sets $P_1 = 0.5$ and $P_2 = 0.5$, experimentation would be expected to yield an 8% higher present value than the status quo management option (Fig. 3). The maximum expected increase in benefits from experimentation over those from the status quo would be 45% (i.e. when P_1 and $P_2 = 1$). The minimum, if there were no responses in body size or survival rate to size-selective fishing, would be -10% (i.e. when P_1 and $P_2 = 0$).

Experimentation would likely yield higher catch biomass than status quo management soon after implementation. By year 8 of an experiment in which there was only an evolutionary response of body size to size-selective fishing, the mean catch biomass from experimental populations would exceed that from populations fished with the status quo strategy (Fig. 4). If survival rate as well as mean weight responds to size-selective fishing, or even if only survival rate responds, the mean catch biomass expected in the experiment would exceed that in the nonexperimental stocks by the second year.

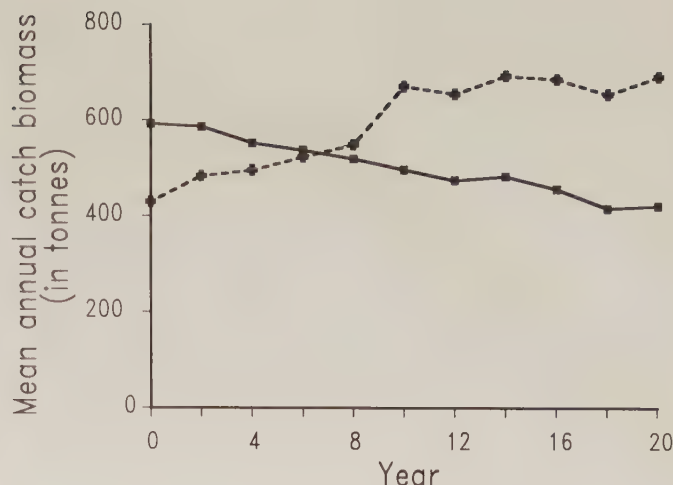


FIG. 4. Forecasts of mean annual catch biomass of even-year pink salmon in size-selective fishing areas when mean adult size responds to size-selective fishing. The broken line reflects the average response in our experiment by selectively harvesting smaller than average size fish whereas the solid line reflects the average response for the status quo policy of continuing to selectively harvest larger than average fish. Standard errors of the means at year 8, for example, are 422 tonnes for the broken line case and 437 tonnes for the solid line case.

Sensitivity Analyses

The discount rate used affected the expected benefit from experimentation and the range of values of P_1 and P_2 for which experimentation was favoured. With an annual discount rate of 5%, the maximum expected present value for the experiment was as much as 60% greater than that for status quo management (Fig. 5A). The minimum was -8%. At a 5% discount rate, experimentation was favoured in 85% of the total parameter space (Fig. 5A, up from 75% in the baseline case, Fig. 3). When the annual discount rate was 15%, the area in which experimentation was favoured decreased to 65% of the total parameter space (Fig. 5B).

However, the most important conclusion from these sensitivity analyses and the baseline results in Fig. 3 is that experimentation is favoured for the most likely range of P_2 ; current literature strongly suggests that P_2 values in the upper half of these figures are more likely to exist in nature. In that range of P_2 , experimentation almost always performs better than status quo management.

When the value for h^2 was set at 0.12 (rather than the 0.22 in the baseline case), and P_1 and $P_2 = 0.5$, the present value of experimentation was 3% greater than that for the status quo. When $h^2 = 0.32$, this difference increased to 13%. Other sensitivity analyses on experimental designs and simulated time horizons usually led to the conclusion that experimentation would have higher present value than not experimenting (McAllister 1990).

Discussion

Our results indicate that economic objectives for management of pink salmon fisheries on the central coast of B.C. might be more readily met by experimentation than by the current management approach, which permits size-selective removal of large fish from each year's population of recruits. As well, McAllister et al. (1992) showed that the proposed experiment could provide a test with high statistical power for the gear selectivity hypothesis and precise and accurate estimates of h^2 .

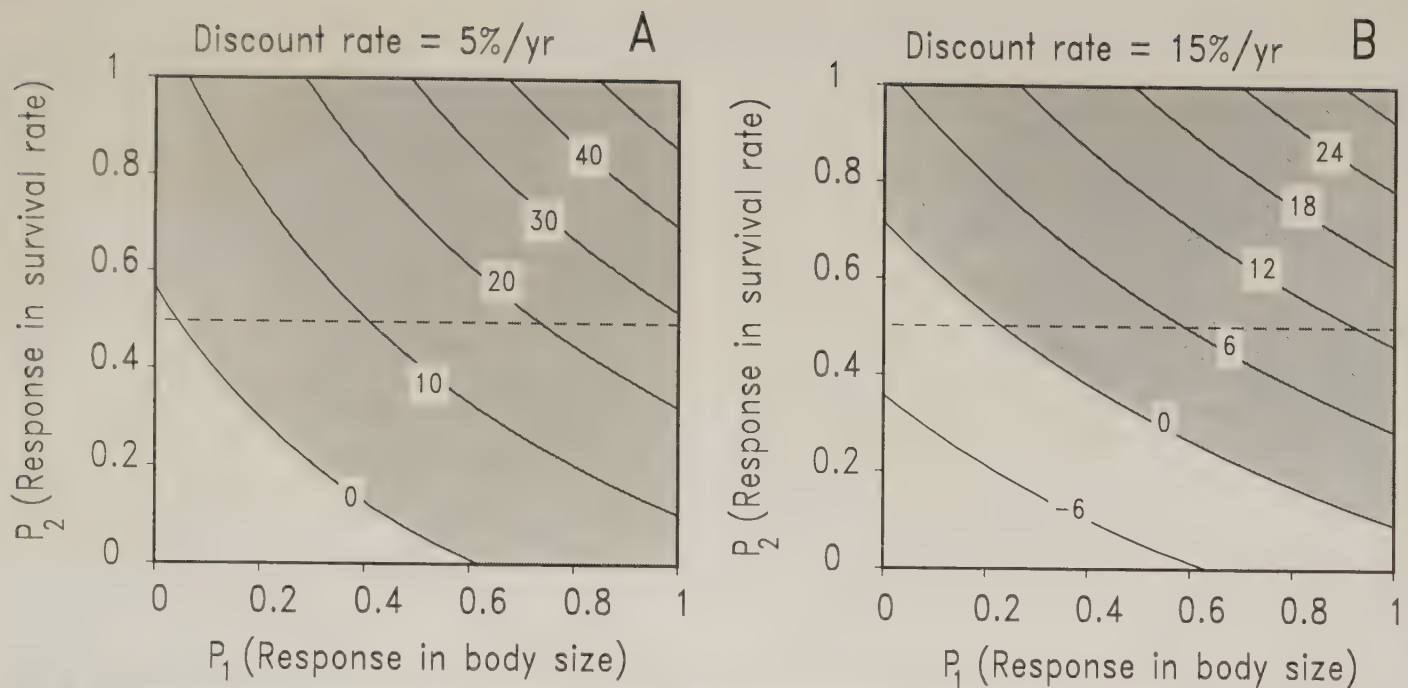


Fig. 5. Isopleths showing the percent increase in present economic value of catches resulting from experimentation compared with the value of catches from status quo management at different levels of P_1 and P_2 . (A) 5% discount rate; (B) 15% discount rate.

in B.C. pink salmon. Thus, unlike situations in many other fisheries (e.g. Allen and Kirkwood 1976), experimental harvest of B.C. pink salmon has potential to yield both information valuable to future management of the fishery and larger economic benefits than the current management approach (i.e. up to a 60% greater present value).

There are several conditions that enhance the anticipated merits of the experimental approach to this problem of decreasing mean adult body weight in B.C. pink salmon. First, as shown in Fig. 3 and 5, there is a low expected cost to experimentation when there is no response in survival rate or body size to size-selective fishing (e.g. for $r = 10\%$, the present value of experimentation is at worst 10% less than that for the status quo, if there is no response to size-selective fishing). Second, there are potentially large costs to status quo management. For example, Ricker et al. (1978) warned of potential commercial extinction of some pink salmon stocks due to lowered reproductive success caused by continued removal of larger pink salmon by fishing gear. Third, net benefits from experimentation might be obtained after relatively few years (i.e., 2–8 yr after initiation of experimentation) because of the short 2-yr life cycle of pink salmon and the potentially large response to size-selective fishing of mean adult weight and egg-to-adult survival rate. Fourth, several potential spatial replicates are available. Fifth, even if the discount rate was high (e.g. 15%), or if the time horizon was only 10 yr (McAllister 1990), or if managers were skeptical (e.g. P_1 and $P_2 < 0.5$) about the two key hypotheses affecting the value of experimentation, the experimental harvest strategy is economically preferable to no experimentation under most of the conditions examined.

Effects of Survival Rate Response on Expected Economic Value of Catches

Even if managers believed that an evolutionary response in mean adult weight to size-selective fishing was unlikely, the

experimental harvest strategy could yield larger present values of catches than the current management approach. Such results could arise from an increasing mean body size of spawners improving spawning success. For example, larger present values were obtained in the simulated experiment than the status quo strategy when $P_1 = 0$, provided that managers placed at least a 60% chance on there being a relationship between egg-to-adult survival rate and mean weight of spawners (i.e. $P_2 = 0.6$ in Fig. 3).

When survival rate was affected by parental body size, the experiment quickly increased it. Allowing larger sized fish to escape from a fishery had an immediate effect on the stock-recruit relationship in the initial year of implementation. More eggs were produced by the larger sized female spawners. But more significantly, the expected number of recruits per spawner increased because of the positive relationship assumed between the egg-to-adult survival rate and the mean body size of spawners (equations (5) and (6)).

Comparison of the Survival Rate Response Model with Empirical Findings

Our results may underestimate the benefits of experimentation for another reason. Under conditions defined in our analysis, the number of recruits per spawner, R/S , increases less rapidly with increased spawner body size (equation (6)) than does female fitness in van den Berghe and Gross' (1989) field study of coho salmon. In their study, female fitness measured by biomass of eggs per female that survive to hatch into fry (f/S) increased as roughly the 5.6 power of the ratio of lengths (i.e. $(70 \text{ cm}/40 \text{ cm})^{5.6} \approx 23$) and the 1.9 power of the ratio of body weights (i.e. assuming that $q = 3$ in the length to weight relationship $W = kL^q$). Thus, if mean spawner weight in even-year stocks increases from 1.220 just prior to experimentation up to 1.925 kg during the experiment, as in some of our simulated experiments, f/S would increase by a factor of 2.38. In contrast, under equation (6) above, our simulated R/S

would increase by a factor of 1.82. For an increase in mean weight from 1.950 to 2.525 kg in odd-year stocks, equation (6) gives an increase in R/S by a factor of 1.10 (this low value results largely from the low value for parameter a of 0.98); based on van den Berghe and Gross (1989), f/S would increase by a factor of 1.63. Hence, equation (6), which relates R/S to spawner body size, gives results more conservative than those found by van den Berghe and Gross (1989).

Other Factors Affecting the Utility of Experimentation

Results from other sensitivity analyses on h^2 , time horizon, and alternative experimental designs also indicated that the experimental strategy had higher expected economic value than the status quo over a wide range of conditions (McAllister 1990). Because the relative benefits of experimentation varied only slightly among different experimental designs, managers could choose from a range of alternative designs.

However, the utility of experimentation could be lower than that reported here for a number of reasons. First, the utility function that reflects managers' responses to risk could be risk-averse rather than risk-neutral, as assumed in the current analysis (Keeney 1977). Second, the actual selection differentials implemented in the design could turn out to be less than the mean value (0.25 kg) used here, for example, because of lower selective efficiency of fishing gear. With a smaller selection differential, mean adult weight could not be expected to increase as much in selectively fished areas. This would result in a smaller annual catch biomass than forecasted for selectively fished areas in the current analysis. Third, the productivity of the stocks employed in the experiment could be lower (or higher) than the productivities estimated by Beacham (1984). For example, Beacham's (1984) estimate for the a parameter for even-year stocks is higher than that for odd-year stocks. This is contrary to our expectation that productivity would be greater for the odd-year pink salmon stocks, which typically have greater average body size than even-year stocks. This discrepancy may be due to sampling error. If actual productivities in either type of stocks are less than the values assumed here, recruitment would respond less to changes in mean adult body size and catch biomass would differ less between the two management options than in the current analysis. Fourth, density-dependent egg-to-adult growth rates could make body size and catch biomass respond less than assumed in the simulations. For example, IPSFC (1984) demonstrated a negative relationship between mean adult weight of Fraser River pink salmon and their annual abundance. Fifth, nets selective for smaller sized fish might selectively catch female pink salmon, which tend to have smaller girths than males (Todd and Larkin 1971). Larger escapements would then be required to achieve the desired female escapement level. Thus, actual catches in experimental groups could be lower than expected.

Costs of Experimentation

As noted above, even if the two key biological hypotheses were false (which is doubtful given current evidence), the present value of experimentation could be only slightly (e.g. 10%) less than that of status quo management. This difference represents a small risk of experimentation or "price of knowledge" (Silvert 1978). There might be additional costs to experimentation which were not included in the analysis (e.g. incremental management costs of the experimental fisheries and capital costs of catching and processing the incremental catch (Ryall 1985)). However, we expect incremental management

and capital costs of experimentation together to be <2% of the total present value of the experiment (see McAllister 1990).

Most importantly, however, the costs of this experiment would be confined to a small area and few stocks, but the general results of the experiment would be applicable coast-wide. Thus, our analysis above probably greatly underestimates the potential value of the experiment when considered on a regional basis.

Costs of Continuing with the Status Quo Strategy

The potential costs of status quo management (i.e. continuing with size-selective harvesting of large fish) are exemplified in Fig. 4 by the systematic decrease in expected catch biomass in selectively fished terminal fisheries. Smaller fish could lead to reduced catches because of lower fecundity and the potentially lower spawning success of smaller sized females (Foerster and Pritchard 1941; Skud 1973; van den Berghe and Gross 1989). Experimentation seems appropriate not only to prevent decreases in catch biomass and commercial extinction of some stocks of pink salmon (Ricker et al. 1978), but also to increase knowledge of the biological dynamics of the fishery and its economic yield. A pilot study would also provide useful prior information on the benefits of applying similar approaches to other salmon resources.

Decision Analysis Method

The decision analysis method used here is a simple, systematic way to conceptualize and evaluate the problem of choosing between experimental and nonexperimental management options. The general results of this decision analysis concur with others for different fisheries situations. Several analyses have suggested that experimental management, when carefully designed, might generate higher expected economic value of catches than nonexperimental options (Sainsbury 1988; Walters and Collie 1989; Welch and Noakes 1990, 1991; Parma and Deriso 1990). However, decision analysis is not intended to replace the decision-making process but rather to assist it by providing information that could enable decision makers to deal with uncertainty in a more objective, rational manner (Clark 1985).

Conclusions

The outlook for experimentation in this case is promising but there are several potential constraints to the implementation of the proposed experimental harvest strategy. For example, it remains unclear whether a sufficient number of fishermen would be interested in participating in the experiment. Fishermen might not be willing participants unless it could be clearly demonstrated that the harvest strategy will quickly result in increasing catch biomass. It also remains unclear whether managers are sufficiently confident in the two key hypotheses to be interested in the proposed harvest strategy.

However, because our analysis strongly suggests that experimentation will have higher expected economic value of harvests than the current policy under most conditions examined, we recommend that managers seriously consider the proposed experimental strategy.

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Statistical Models for Estimating CPUE from Catch and Effort Data

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Catch-per-unit-effort (CPUE) provides one of the most commonly used abundance indices in fishery research. The literature, however, offers no unique method of estimating CPUE and its variance from catch and effort data. In this paper we develop two models (univariate and bivariate) that generalize previous approaches and remain valid under management restrictions on catch and/or effort. Both models estimate CPUE from measures of central tendency in the underlying catch and effort distributions. The models involve normalizing transformation parameters that, along with other parameters, are estimated by maximum likelihood. We illustrate the models using data from Pacific ocean perch (*Sebastes alutus*). For the four data sets examined, the univariate and bivariate models result in similar estimates of CPUE. However, other commonly used CPUE measures lead to inconsistent results, in particular for data sets in which catch was restricted by low trip limits. We recommend the bivariate model, since it accounts for the bivariate structure of catch and effort data. Furthermore, it can easily be adapted to accommodate alternative indices, for example, the effort required to attain a specified catch.

Les prises par unité d'effort (PUE) constituent l'un des indices d'abondance les plus couramment utilisés dans les recherches sur les pêches. On ne trouve cependant pas dans les publications de méthode unique pour estimer le PUE et sa variance à partir des données sur les prises et l'effort. Nous présentons ici deux modèles (univarié et bivarié) qui généralisent les approches faites antérieurement et demeurent valides en dépit de limites de gestion portant sur les prises ou l'effort. Les deux modèles permettent d'estimer le PUE à partir de la tendance centrale des distributions sous-jacentes des prises et de l'effort. Les modèles comportent des paramètres de transformation normalisateurs qui, avec d'autres paramètres, sont estimés par maximum de vraisemblance. Nous démontrons le fonctionnement des modèles à l'aide de données sur le sébaste du Pacifique (*Sebastes alutus*). Pour les quatre ensembles de données examinées, le modèle univarié et le modèle bivarié donnent des valeurs estimées de PUE semblables. Par ailleurs, les autres mesures du PUE couramment utilisées donnaient des résultats variables, notamment pour les ensembles de données pour lesquelles les prises étaient limitées à de faibles valeurs par sortie de pêche. Nous recommandons l'utilisation du modèle bivarié car il permet de tenir compte de la structure bivariée des données sur les prises et l'effort. De plus, il peut facilement être adapté à d'autres indices, par exemple l'effort nécessaire à l'atteinte d'un niveau de prises donné.

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Catch and effort data are fundamental to fish stock assessments. For many fisheries, catch-per-unit-effort (CPUE) data comprise the main abundance index. Even when other indices are available, CPUE data still provide an important assessment tool. In modern catch-age analysis (Megrey 1989), for example, catch-age data alone are insufficient to estimate both abundance and fishing mortality (Pope and Shepherd 1982; Deriso et al. 1985; Tanaka 1989) and auxiliary data such as CPUE are often used. Here, our goal is to develop a general method for estimating CPUE and its variance. We employ models that generalize previous estimation methods and are applicable under management restrictions on catch and/or effort.

Analysis of CPUE data often involves comparisons among indices obtained under differing circumstances. For example, Gulland (1956) and Beverton and Holt (1957) recognized that CPUE may differ among vessels, dependent on characteristics such as the tonnage class. Their work was later expanded by Robson (1966), and the more recent methods of Gavaris (1980) and Kimura (1981) are now commonly applied. Other authors (Peterman and Steer 1981; Bannerot and Austin 1983; Richards and Schnute 1986) have compared CPUE with different abundance indices. Often, these relationships appear nonlinear, perhaps due to factors such as the behavior of fish and fishermen

(Gulland 1964; Rothschild 1977). Richards and Schnute (1986), Richards (1987), and Schnute et al. (1990) have used errors-in-variables methods to investigate such relationships.

All analyses described above must, of course, begin with the calculation of CPUE itself. Ideally, each CPUE estimate should be accompanied with a confidence interval, particularly if errors-in-variables methods are used to compare abundance indices. At this level of detail, the estimation problem is defined by a single stratum, for example, a particular target species, fishing ground, year, and gear type. A typical data record might represent one set, day, or trip. We let $C = \{C_i\}_{i=1, \dots, n}$ and $E = \{E_i\}_{i=1, \dots, n}$ represent vectors of catch and effort, respectively, where i indexes the data record. Typically, CPUE for the stratum is calculated as the ratio of sums $\sum C_i / \sum E_i$, or equivalently, as the ratio of means $\bar{C} / \bar{E}$, according to the methods of ratio estimators (Cochran 1977, chap. 6). Another approach has been to determine

$$(0.1) \quad I_i = C_i / E_i$$

and to estimate the mean and variance of CPUE from the I -distribution. The lognormal (Gavaris 1980), root normal (Quinn 1985), and negative binomial (Bannerot and Austin 1983) have provided adequate descriptions of the I -distribution

in different contexts. Alternatively, one might examine the median and quantiles of the I -distribution.

In this paper we approach the estimation of CPUE from two points of view, and we develop a model to accommodate each view. The first view (univariate model) is that of the single univariate series $I = \{I_i\}$, with CPUE computed from its central tendency. The second view (bivariate model) considers both data vectors E and C simultaneously. Previous analyses have treated E and C as separate univariate series, with CPUE computed from the central tendency of each series, for example, from the two means or medians. Here, we recognize E_i and C_i as correlated random variables and determine CPUE from the central tendency of the bivariate (E, C) -distribution.

Our univariate and bivariate models have several advantages. Since we use maximum likelihood methods (Edwards 1972; Kendall and Stuart 1979), confidence intervals can be estimated for important model parameters. Thus, statistical comparisons are possible among CPUE indices. Furthermore, we acknowledge that normalizing transformations may be required and transformation parameters are estimated simultaneously with other model parameters. The model is still applicable when a change to the fishery alters the shape of the I - or (E, C) -distribution. The bivariate model has the additional benefit that it avoids loss of information due to data reduction. It deals directly with the data pair (E_i, C_i) , rather than the one-dimensional ratio I_i in equation (0.1). Catch-effort relationships are also a consequence of the bivariate distribution, for example, estimates of predicted catch conditioned on effort or predicted effort conditioned on catch.

We illustrate our models using data from a stock of Pacific ocean perch (*Sebastes alutus*). In recent years, restrictions on the fishery for this stock have included trip limits. A trip limit is a ceiling placed on the allowable catch by a vessel during one fishing trip. Our methods accommodate such restrictions on catch. We also display graphical results from our models. These diagrams portray the structure of catch and effort data and the effect of trip limits on both data structure and model parameters.

Section 1 of this paper presents the univariate and bivariate models in a general context. Possible inferences on model parameters are discussed in section 2, and the models are related more specifically to CPUE data in section 3. In section 4 we apply the models to CPUE data from Pacific ocean perch, collected under management regimes without a trip limit and with a 9-t trip limit. Numerous model equations are presented in tables. We identify equations in the tables with square brackets to distinguish them from equations in the text, numbered with parentheses.

1. Statistical Model

We must discuss a number of technical points to state the univariate and bivariate models rigorously. However, our models are conceptually simple. The first step involves a modified power transformation to normalize the data. The transformation also includes user-selected scaling parameters which simplify statistical interpretation of the results. For univariate data such as (0.1), CPUE is determined from the median of the normalized distribution. Transformed bivariate data are assumed to follow a binormal distribution, and CPUE is determined from the distribution medians. Our work generalizes the model of Quinn (1985) who used a root normal distribution, that is, a transformation exponent of 0.5. The examples in section 4 illustrate geometrically why such generalizations are needed.

We begin by defining the models in terms of generic data vectors $x = \{x_i\}_{i=1, \dots, n}$ and $y = \{y_i\}_{i=1, \dots, n}$. These could represent I , E , or C , depending on the context. Since catch and effort data are typically skewed, transformations are required. For example, Quinn (1985) used the Box-Cox transformation

$$(1.1) \quad \xi_i = \begin{cases} \frac{x_i^\alpha - 1}{\alpha}, & \alpha \neq 0 \\ \ln(x_i), & \alpha = 0 \end{cases}$$

(Box and Cox 1964). We use instead the transformations

$$(1.2) \quad \xi_i = \begin{cases} \frac{x_i^\alpha - u^\alpha}{U^\alpha - u^\alpha}, & \alpha \neq 0 \\ \frac{\ln(x_i/u)}{\ln(U/u)}, & \alpha = 0 \end{cases}$$

$$(1.3) \quad \eta_i = \begin{cases} \frac{y_i^\beta - v^\beta}{V^\beta - v^\beta}, & \beta \neq 0 \\ \frac{\ln(y_i/v)}{\ln(V/v)}, & \beta = 0 \end{cases}$$

adapted from Schnute and McKinnell (1984). The exponents (α, β) in (1.2)–(1.3) act as transformation parameters, while the prescribed quantities (u, U, v, V) are selected by the user to scale the data. The values u and v are chosen to represent typical low values of x_i and y_i , respectively; similarly, U and V are chosen to represent typical high values of x_i and y_i . Thus, most transformed observations ξ_i and η_i lie within the range $(0, 1)$.

The transformations (1.2)–(1.3) honor the dimensions of x and y , unlike the classical Box-Cox transformations. For example, (1.1) involves subtracting the dimensionless number 1 from the dimensioned quantity x_i^α . By contrast, (1.2) defines ξ_i as a legitimate dimensionless number. Furthermore, the mean of ξ_i in (1.2) remains relatively constant as α varies whereas the mean in (1.1) can be highly correlated with the choice of α .

The univariate model consists of the transformation (1.2) and the assumption that the ξ_i ($i = 1, \dots, n$) are independent and normally distributed:

$$(1.4) \quad \xi_i \sim N(\mu, \sigma^2).$$

The symbol $N(\mu, \sigma^2)$ denotes a normal distribution with mean μ and variance σ^2 . Equation [1.3] (Table 1) explicitly defines the corresponding probability density function (pdf) $p(\xi|\mu, \sigma)$. Given user choices for u and U , the three parameters

$$(1.5) \quad \theta = (\alpha, \mu, \sigma)$$

determine the univariate model. The pdf for the univariate model, $p(x|\theta)$ in [1.4], is the product of $p(\xi|\mu, \sigma)$ and the partial derivative $\partial \xi / \partial x$ from (1.2).

By analogy with the univariate model (1.2) and (1.4), the bivariate model consists of both transformations (1.2)–(1.3) and the assumption that the pairs (ξ_i, η_i) , $i = 1, \dots, n$, are independent and binormal:

$$(1.6) \quad (\xi_i, \eta_i) \sim B(\mu, v, \rho, \sigma^2, \tau^2).$$

Here, the symbol $B(\mu, v, \rho, \sigma^2, \tau^2)$ refers to a binormal distribution with pdf given by $q(\xi, \eta|\mu, v, \rho, \sigma, \tau)$ in [1.5]. It is characterized by the mean μ and variance σ^2 of the first variate ξ ,

TABLE 1. Probability density functions for the univariate and bivariate models. Continuous extensions to the cases $\alpha = 0$ and $\beta = 0$ are shown in (1.2)–(1.3).

$$\begin{aligned}
 [1.1] \quad \xi(x) &= \frac{x^\alpha - u^\alpha}{U^\alpha - u^\alpha} \\
 [1.2] \quad \eta(y) &= \frac{y^\beta - v^\beta}{V^\beta - v^\beta} \\
 [1.3] \quad p(\xi|\mu, \sigma) &= \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{1}{2}\left[\frac{\xi-\mu}{\sigma}\right]^2} \\
 [1.4] \quad p(x|\boldsymbol{\theta}) &= p(\xi(x)|\mu, \sigma) \frac{\partial \xi(x)}{\partial x} \\
 [1.5] \quad q(\xi, \eta|\mu, v, \rho, \sigma, \tau) &= \frac{1}{2\pi\sigma\tau\sqrt{1-\rho^2}} e^{-\frac{1}{2(1-\rho^2)}\left[\left(\frac{\xi-\mu}{\sigma}\right)^2 - 2\rho\frac{\xi-\mu}{\sigma}\frac{\eta-v}{\tau} + \left(\frac{\eta-v}{\tau}\right)^2\right]} \\
 [1.6] \quad q(x, y|\boldsymbol{\Phi}) &= q(\xi(x), \eta(y)|\mu, v, \rho, \sigma, \tau) \frac{\partial \xi(x)}{\partial x} \frac{\partial \eta(y)}{\partial y}
 \end{aligned}$$

TABLE 2. Relationships between the bivariate parameters in equations (1.8)–(1.9) and the new parameters in (1.10)–(1.11).

$$\begin{aligned}
 [2.1] \quad a_0 &= \mu - a_1 v \\
 [2.2] \quad b_0 &= v - b_1 \mu \\
 [2.3] \quad a_1 &= \rho\sigma/\tau \\
 [2.4] \quad b_1 &= \rho\tau/\sigma
 \end{aligned}$$

the mean v and variance τ^2 of the second variate η , and the correlation ρ between ξ and η . The full parameter vector

$$(1.7) \quad \boldsymbol{\Phi} = (\alpha, \beta, \mu, v, \rho, \sigma, \tau)$$

for this model includes the two transformation parameters (α, β) and the five binormal parameters $(\mu, v, \rho, \sigma, \tau)$. The pdf of the bivariate model, $q(x, y|\boldsymbol{\Phi})$ in [1.6], requires the partial derivatives $\partial \xi / \partial x$ and $\partial \eta / \partial y$ from the transformations (1.2)–(1.3).

One feature of the binormal distribution is that the conditional means (expected values)

$$(1.8) \quad \text{Exp}[\xi_i|\eta_i] = \mu + \frac{\rho\sigma}{\tau} (\eta_i - v)$$

$$(1.9) \quad \text{Exp}[\eta_i|\xi_i] = v + \frac{\rho\tau}{\sigma} (\xi_i - \mu),$$

given a value of the other variate, are linearly dependent on that value (Kendall et al. 1987, p. 523–524). Thus, they can be formulated more simply as

$$(1.10) \quad \text{Exp}[\xi_i|\eta_i] = a_0 + a_1 \eta_i$$

$$(1.11) \quad \text{Exp}[\eta_i|\xi_i] = b_0 + b_1 \xi_i,$$

respectively, where [2.1]–[2.4] (Table 2) express the new parameters (a_0, a_1, b_0, b_1) in terms of the binormal parameters $(\mu, v, \rho, \sigma, \tau)$. As we demonstrate below, (1.10)–(1.11) can be useful expressions for catch–effort relationships.

Our analysis requires the three additional parameters

$$(1.12) \quad x^* = [\mu(U^\alpha - u^\alpha) + u^\alpha]^{\frac{1}{\alpha}}$$

$$(1.13) \quad y^* = [v(V^\beta - v^\beta) + v^\beta]^{\frac{1}{\beta}}$$

$$(1.14) \quad \lambda^* = y^*/x^*.$$

Here, x^* is the value x_i in (1.2) that results in the value $\xi_i = \mu$. By analogy, y^* is the value y_i in (1.3) that results in the value $\eta_i = v$. In the univariate model, μ simultaneously represents the mean, median, and mode of the variate ξ . Also, if $\alpha = 1$, then x^* represents the mean, median, and mode of the variate x . When $\alpha \neq 1$, the variate x is not normal and x^* represents the median only. Similarly, the parameter pair (x^*, y^*) describes the (x, y) -medians of the bivariate model. Therefore, λ^* can be interpreted as a ratio of medians.

To put these remarks in a broader context, notice that the transformation $x = f(\xi)$ defined by the inverse of (1.2) is nonlinear (except when $\alpha = 1$). A nonlinear function $f(\cdot)$ does not generally preserve measures of central tendency, such as the mean or mode. Thus, if μ is the mean of ξ , $f(\mu)$ is not usually the mean of x . Since f is monotone, it does correctly transform quantiles, including the median. We adopt the median x^* as a parameter because it corresponds naturally to the most obvious measure μ of central tendency in the normalized variate ξ . We stress, however, that the parameter x^* should not be confused with the sample median, which is a statistic associated with a specific data set.

To obtain inferences on x^* and y^* , some reparameterization is required. For the univariate model, the pair (α, μ) can be replaced by (α, x^*) in $\boldsymbol{\theta}$ in (1.5). More generally,

$$(1.15) \quad (\alpha, \mu) \leftrightarrow (\alpha, x^*),$$

that is, these two parameter pairs are equivalent. For a given α , x^* is computed from μ by (1.12); conversely, the transformation (1.2) determines μ from x^* . A similar equivalence for the bivariate model is

$$(1.16) \quad (\alpha, \beta, \mu, v) \leftrightarrow (\alpha, \beta, x^*, \lambda^*).$$

The transition from left to right employs (1.12)–(1.14), while the reverse transition uses (1.14) and (1.2)–(1.3).

TABLE 3. Minimizations of $K(\theta)$ and $L(\Phi)$ for inferences about parameter subsets.

[3.1]	$K_1(\alpha, \mu) = \min_{\sigma} K(\alpha, \mu, \sigma)$
[3.2]	$K_2(\alpha) = \min_{\mu, \sigma} K(\alpha, \mu, \sigma)$
[3.3]	$K_3(x^*) = \min_{\alpha, \sigma} K(\alpha, x^*, \sigma)$
[3.4]	$L_1(\alpha, \beta, \mu, \nu) = \min_{\rho, \sigma, \tau} L(\alpha, \beta, \mu, \nu, \rho, \sigma, \tau)$
[3.5]	$L_2(\alpha, \beta) = \min_{\mu, \nu, \rho, \sigma, \tau} L(\alpha, \beta, \mu, \nu, \rho, \sigma, \tau)$
[3.6]	$L_3(\lambda^*) = \min_{\alpha, \beta, x^*, \rho, \sigma, \tau} L(\alpha, \beta, x^*, \lambda^*, \rho, \sigma, \tau)$

2. Statistical Inference

Likelihood methods (Edwards 1972; Kendall and Stuart 1979, chap. 18) can be used for making inferences on all parameters in the models described above. Because these methods provide a unified framework for the entire analysis, we adopt them here. In particular, we use parametric maximum likelihood, rather than nonparametric sample medians, to estimate x^* , y^* , and λ^* . In worked examples below, we provide comparisons between parametric and nonparametric results.

The likelihood for the univariate model, that is, the probability of observing x given θ , is

$$(2.1) \quad P(x|\theta) = \prod_{i=1}^n p(x_i|\theta),$$

the product of the pdf [1.4] over components x_i of the data vector x . For statistical inference, we use twice the negative log likelihood

$$(2.2) \quad K(\theta) = -2 \ln [P(x|\theta) - n \ln(2\pi)].$$

The constant $n \ln(2\pi)$ can be subtracted, since the analysis depends entirely on relative values of $K(\theta)$. Given choices of the prescribed quantities (u, U) in (1.2), the minimum of $K(\theta)$ defines the maximum likelihood estimates $\hat{\theta} = (\hat{\alpha}, \hat{\mu}, \hat{\sigma})$ or equivalently, $\hat{\theta} = (\hat{\alpha}, \hat{x}^*, \hat{\sigma})$ by (1.15).

The likelihood analysis also requires certain minimizations of $K(\theta)$, as defined by [3.1]–[3.3] (Table 3). For example, $K_1(\alpha, \mu)$ in [3.1] could be used to examine the joint confidence in (α, μ) by treating σ as a nuisance parameter. Similarly, a confidence interval for α could be obtained from $K_2(\alpha)$ in [3.2]. The definition $K_3(x^*)$ in [3.3] uses the equivalence (1.15). It follows from [3.1] that

$$(2.3) \quad K_3(x^*) = \min_{\alpha} K_1(\alpha, x^*)$$

provides an alternative expression for $K_3(x^*)$.

The functions $K(\theta)$, $K_1(\alpha, \mu)$, and $K_2(\alpha)$ can also be expressed analytically in terms of the moments ξ in [4.3] and m_{20} in [4.5] (Table 4). Equations [5.3]–[5.5] (Table 5) list the resulting expressions, where the moments have been written as a function of α to emphasize their dependency on the transformation exponent. Although the function $K_3(x^*)$ cannot be represented analytically in this fashion, it can be computed numerically from (2.3).

Statistical inferences on the univariate parameters may be obtained from functions [3.2]–[3.3]. For example, values of

TABLE 4. Moment statistics for the vectors x , y , ξ , and η .

[4.1]	$x' = \left[\prod_{i=1}^n x_i \right]^{\frac{1}{n}}$
[4.2]	$y' = \left[\prod_{i=1}^n y_i \right]^{\frac{1}{n}}$
[4.3]	$\bar{\xi} = \frac{1}{n} \sum_{i=1}^n \xi_i$
[4.4]	$\bar{\eta} = \frac{1}{n} \sum_{i=1}^n \eta_i$
[4.5]	$m_{ij} = \frac{1}{n} \sum_{k=1}^n (\xi_k - \bar{\xi})^i (\eta_k - \bar{\eta})^j$

$K_3(x^*)$ define approximate confidence intervals (or inference intervals in the sense of Bates and Watts (1988, p. 7)). Changes in $K_3(x^*)$ can be scaled to probability units by the χ^2 distribution, since minus twice a difference in log likelihoods is asymptotically χ^2 distributed. Thus, the equation

$$(2.4) \quad K_3(x^*) = K_3(\hat{x}^*) + \chi_p^2(1)$$

determines an approximate p -level confidence interval for x^* , where $\chi_p^2(1)$ denotes the value of the χ^2 distribution at probability level p with 1 df. Similarly,

$$(2.5) \quad K_2(\alpha) = K_2(\hat{\alpha}) + \chi_p^2(1)$$

defines an approximate p -level confidence interval for α . In general, confidence intervals are asymmetric, reflecting model nonlinearities.

The likelihood function for the bivariate model (1.2)–(1.3) and (1.6) is given by

$$(2.6) \quad Q(x, y|\Phi) = \prod_{i=1}^n q(x_i, y_i|\Phi),$$

the product of the pdf [1.6] over all data pairs (x_i, y_i) . Again, statistical inference is based on twice the negative log likelihood

$$(2.7) \quad L(\Phi) = -2 \ln [Q(x, y|\Phi)] - 2n \ln(2\pi).$$

The minimum of $L(\Phi)$ defines the maximum likelihood estimates

$$\hat{\Phi} = (\hat{\alpha}, \hat{\beta}, \hat{\mu}, \hat{\nu}, \hat{\rho}, \hat{\sigma}, \hat{\tau}),$$

given the choices (u, U, v, V) in (1.2)–(1.3). The additional estimates

$$(\hat{a}_0, \hat{a}_1, \hat{b}_0, \hat{b}_1, \hat{x}^*, \hat{y}^*, \hat{\lambda}^*)$$

are then determined by [2.1]–[2.4] and (1.12)–(1.14).

Our analysis requires several minimizations of $L(\Phi)$, given by the definitions [3.4]–[3.6]. The definition of $L_3(\lambda^*)$ in [3.6] utilizes the equivalence (1.16). The alternative expression

$$(2.8) \quad L_3(\lambda^*) = \min_{\alpha, \beta, x^*} L_1(\alpha, \beta, x^*, \lambda^*)$$

from [3.4] and (1.16) may be used to obtain $L_3(\lambda^*)$ numerically. Analytical expressions of $L(\Phi)$, $L_1(\alpha, \beta, \mu, \nu)$, and $L_2(\alpha, \beta)$ are listed in equations [5.6]–[5.8], respectively, based on the moments [4.1]–[4.5].

TABLE 5. Inference functions (twice the negative log likelihood) for the univariate and bivariate models. Expressions [5.1] and [5.2] are related to the partial derivatives $\partial\hat{\xi}/\partial x$ and $\partial\hat{\eta}/\partial y$ in [1.4] and [1.6].

[5.1]	$J_x(\alpha) = (\alpha - 1) \ln(x') - \ln \left[\frac{U^\alpha - u^\alpha}{\alpha} \right]$
[5.2]	$J_y(\beta) = (\beta - 1) \ln(y') - \ln \left[\frac{V^\beta - v^\beta}{\beta} \right]$
[5.3]	$K(\theta) = n \ln(\sigma^2) + \frac{n}{\sigma^2} \{ [\bar{\xi}(\alpha) - \mu]^2 + m_{20}(\alpha) \} - 2n J_x(\alpha)$
[5.4]	$K_1(\alpha, \mu) = n \ln \{ [\bar{\xi}(\alpha) - \mu]^2 + m_{20}(\alpha) \} + n[1 - 2 J_x(\alpha)]$
[5.5]	$K_2(\alpha) = n \ln[m_{20}(\alpha)] + n[1 - 2 J_x(\alpha)]$
[5.6]	$L(\Phi) = n \ln[\sigma^2 \tau^2 (1 - \rho^2)] + \frac{n}{1 - \rho^2} \left\{ \left[\frac{\bar{\xi}(\alpha) - \mu}{\sigma} \right]^2 - 2\rho \frac{[\bar{\xi}(\alpha) - \mu][\bar{\eta}(\beta) - v]}{\sigma\tau} + \left[\frac{\bar{\eta}(\beta) - v}{\tau} \right]^2 \right\} + \frac{n}{1 - \rho^2} \left\{ \frac{m_{20}(\alpha)}{\sigma^2} - 2\rho \frac{m_{11}(\alpha, \beta)}{\sigma\tau} + \frac{m_{02}(\beta)}{\tau^2} \right\} - 2n[J_x(\alpha) + J_y(\beta)]$
[5.7]	$L_1(\alpha, \beta, \mu, v) = n \ln \{ [(\bar{\xi}(\alpha) - \mu)^2 + m_{20}(\alpha)][(\bar{\eta}(\beta) - v)^2 + m_{02}(\beta)] - [(\bar{\xi}(\alpha) - \mu)(\bar{\eta}(\beta) - v) + m_{11}(\alpha, \beta)]^2 \} + 2n[1 - J_x(\alpha) - J_y(\beta)]$
[5.8]	$L_2(\alpha, \beta) = n \ln \{ m_{20}(\alpha)m_{02}(\beta) - [m_{11}(\alpha, \beta)]^2 \} + 2n[1 - J_x(\alpha) - J_y(\beta)]$

Statistical inferences on bivariate parameters may be obtained from functions [3.5]–[3.6]. The equation

$$(2.9) \quad L_3(\lambda^*) = L_3(\hat{\lambda}^*) + \chi_p^2(1),$$

analogous to (2.4), determines an approximate p -level confidence interval for λ^* . An approximate p -level confidence region for (α, β) is defined as the interior of the contour

$$(2.10) \quad L_2(\alpha, \beta) = L_2(\hat{\alpha}, \hat{\beta}) + \chi_p^2(2),$$

where $\chi^2(2)$ denotes a χ^2 distribution with 2 df.

As we have explained, the user-defined constants (u, U, v, V) serve to locate and scale the transformed data (ξ, η) approximately within the range $(0, 1)$. Changes in these constants induce natural transformations on the parameters (μ, v, σ, τ) , consistent with the corresponding changes in (ξ, η) . For specified (α, β) , however, such changes have no effect on $(x^*, y^*, \lambda^*, \rho)$, which relate directly to features in the original (x, y) -data. In effect, (μ, v, σ, τ) act as nuisance parameters in a model designed primarily for $(\alpha, \beta, x^*, y^*, \lambda^*, \rho)$. Partly for this reason, we have introduced the equivalences (1.15) and (1.16) and the minimizations K_2 , K_3 , L_2 , and L_3 . Richards and Schnute (1990, p. 1152) give further analytical details in a somewhat different context.

The discussion so far has avoided a technical point which makes our models somewhat more complex. The normal and binormal assumptions (1.4) and (1.6) assume that the variates ξ and η span the entire real range $(-\infty, \infty)$. In the case of non-zero exponents α or β , the transformations (1.2)–(1.3) are bounded by critical values

$$(2.11) \quad c_\xi = -\frac{u^\alpha}{U^\alpha - u^\alpha}$$

$$(2.12) \quad c_\eta = -\frac{v^\beta}{V^\beta - v^\beta}.$$

For example, the range of ξ is given by $(-\infty, c_\xi)$ when $\alpha < 0$,

$(-\infty, \infty)$ when $\alpha = 0$, and (c_ξ, ∞) when $\alpha > 0$. Similarly, when β is negative, zero, or positive, the range of η is $(-\infty, c_\eta)$, $(-\infty, \infty)$, or (c_η, ∞) , respectively. Thus, some of our model equations are only approximate, since they fail to account for truncations in ξ and η . The Appendix describes more precise models which take these truncations into account. In this formulation, μ and v no longer represent exact medians. We demonstrate, however, that the truncation corrections have no practical significance to our results below.

3. Model Application

We next relate the generic models in section 1 to catch and effort data. The univariate model is applied to the CPUE series I , defined by (0.1). The model consists of equations (1.2) and (1.4), where I_i is substituted for x_i in (1.2). Similarly, the bivariate model is applied to the series C and E of catch and effort data. The model then consists of equations (1.2), (1.3), and (1.6), where E_i is substituted for x_i in (1.2) and C_i for y_i in (1.3). The univariate and bivariate models are not necessarily self-consistent. For example, if the (E, C) -distribution is specified by our bivariate model, then the distribution of $I = C/E$ is determined. Such a distribution will generally not conform to the assumptions of our univariate model. However, the univariate model may provide an adequate approximation.

A critic of the bivariate model might argue that one or other of the variables is controlled, and therefore that either E_i or C_i is not random. We recognize that catch and/or effort limitations apply to many fisheries. Such limitations rarely act as deterministic controls, however, except perhaps under experimental conditions. In a fishery, the observations E_i and C_i both contain uncontrolled variability, although limitations may affect the central tendency of E or C . Thus, both variables must be considered random from the point of view of an analyst.

A complete description of the catch–effort models requires additional notation. For the univariate model, we let I^* denote the distribution median and $\hat{I}^*$ the maximum likelihood estimate of I^* . The sample mean and median of I are indicated by

$\bar{I}$ and $\bar{I}^*$, respectively. In general, the quantities I^* , $\hat{I}^*$, $\tilde{I}^*$, and $\bar{I}$ all differ. For example, I^* is a parameter of the distribution of the variate I , where the probability that $I < I^*$ (or that $I > I^*$) is 50%. The estimate $\hat{I}^*$ of I^* is obtained by maximum likelihood, based on the data vector I . The sample median $\tilde{I}^*$ of I provides another estimate of I^* , usually different from $\hat{I}^*$. Both the sample median $\tilde{I}^*$ and sample mean $\bar{I}$ measure central tendency for I . However, these two measures can differ considerably in highly skewed distributions.

For the bivariate model, (E^*, C^*) denote parametric medians of the joint (E, C) -distribution, and $(\hat{E}^*, \hat{C}^*)$ represent the maximum likelihood estimates of (E^*, C^*) . From (1.14), define

$$(3.1) \quad \lambda^* = C^*/E^*.$$

The maximum likelihood estimate for λ^* is then

$$(3.2) \quad \hat{\lambda}^* = \hat{C}^*/\hat{E}^*.$$

We also define two other estimates of central tendency in the bivariate distribution:

$$(3.3) \quad \bar{\lambda}^* = \bar{C}/\bar{E} = \sum_i C_i / \sum_i E_i$$

$$(3.4) \quad \tilde{\lambda}^* = \tilde{C}/\tilde{E},$$

where $\bar{C}$ and $\bar{E}$ denote the sample means of the univariate series C and E , respectively, and $\tilde{C}$ and $\tilde{E}$ denote the corresponding sample medians.

The purpose of our paper is to develop models for estimating CPUE and associated confidence intervals. Any of the measures of central tendency just described could serve as potential CPUE indices. In the context of the univariate model, we measure CPUE by the parameter I^* and obtain the estimate $\hat{I}^*$. Similarly, within the bivariate model, we use λ^* to measure CPUE and obtain the estimate $\hat{\lambda}^*$. Since both estimates $\hat{I}^*$ and $\hat{\lambda}^*$ are derived from parametric models, we can use likelihood inference (section 2) to accomplish the paper's goals. The other suggested estimators ($\tilde{I}^*$, $\tilde{\lambda}^*$, $\bar{\lambda}^*$) are essentially nonparametric.

One aspect of the bivariate model is that it contemplates a catch-effort relationship, and conversely, an effort-catch relationship. In transform space, the relationships are linear, as indicated by expressions (1.10)–(1.11). In catch-effort space, the relationships are curvilinear, conforming to the curve types described by Schnute and Jensen (1986). These monotone curves may have nonzero intercepts and asymptotes along either the catch or effort axis. For example, a positive intercept along the catch axis would suggest that the smallest unit of effort leads to a measurable catch. If a large effort is required to obtain any catch, then the curve might have a positive intercept along the effort axis. Confidence bands could also be computed for these curves, following methods described in a different context by Richards and Schnute (1990).

4. Rockfish Example

4A. Data Sources

To illustrate the model, we have selected four years of data from the Goose Island Gully stock of Pacific ocean perch. The particular years were chosen because of large sample sizes (at least 50 records) and different fishery restrictions. For two of these years, 1977 and 1980, there was no limit to the allowed catch of Pacific ocean perch during a fishing trip. However, for the other two years, 1987 and 1989, trip limits played a

major role in the management regime. During 1987, a 9-t trip limit was in effect. During 1989, there were several trip limits, but we only include data collected under a 9-t limit.

Goose Island Gully is a submarine canyon located in Queen Charlotte Sound, British Columbia. The Goose Island Gully stock of Pacific ocean perch was heavily targeted by Soviet trawlers in the late 1960s and Japanese trawlers in the early 1970s. By the late 1970s, the stock had been severely depleted (Ketchen 1981; Kimura 1981; Archibald et al. 1983). The stock is now fished by Canadian trawlers only, which are regulated by quotas, seasonal closures, and a series of trip limits. Between 1977 and 1990, the annual catch averaged 1.1 kt. Here, we use the term "catch" to refer to landed biomass, recognizing that discards may have occurred at sea.

A data record represents the Pacific ocean perch catch and corresponding trawl hours (effort) by a vessel during a fishing trip to Goose Island Gully. To account for the multispecies nature of the rockfish trawl fishery, a record was included in the analysis only if Pacific ocean perch comprised more than 20% of the total catch by weight. Furthermore, we used only records verified by logbooks and/or interviews. Information on trip limits was obtained from notices to industry. If the regulation changed during a fishing trip, the higher of the two limits was assumed to be the one in effect. We excluded a few records with a Pacific ocean perch catch greater than 150% of the trip limit. We assumed that these vessels were either violating the regulations or fishing in an adjacent area with a higher trip limit. In both 1987 and 1989, 23-t trip limits applied to adjacent stocks, and management areas did not precisely coincide with stock boundaries.

4B. Analysis of Catch-Effort Data

The univariate series I was determined from (0.1) for each of the four years of Pacific ocean perch data. The resulting data are highly skewed and the corresponding histograms have long tails (Fig. 1). In each case, the tail has been accentuated by one outlying point. The histogram shapes differ little between years without trip limits (Fig. 1A and 1B) and years with trip limits (Fig. 1C and 1D).

In contrast with the univariate data, scatter plots of the corresponding bivariate data (E_i, C_i) clearly reflect the influence of trip limits (Fig. 2). A distinct relationship between catch and effort is apparent in Fig. 2A and 2B. The range of catch is greatly reduced for Fig. 2C and 2D, and the data tend to concentrate along the line $C = 9$ t, the magnitude of the trip limit. The range of effort is also reduced, but to a lesser extent. This data concentration weakens any dependence of catch on effort. The four outliers from the univariate series correspond to points with a high value C_i relative to E_i , but do not appear as isolated from the rest of the data as they do in Fig. 1.

Nonlinear techniques are required to estimate parameters of the univariate and bivariate models. We applied the simplex search method (Nelder and Mead 1965; Mittertreiner and Schnute 1985; Press et al. 1986) to obtain the estimates $(\hat{\theta})$ and $(\hat{\Phi})$ (Table 6). Estimates $(\hat{\alpha}, \hat{\beta}, \hat{E}^*, \hat{C}^*, \hat{\lambda}^*, \hat{\rho})$ for the bivariate model all appear to depend on trip limits. In particular, values of $\hat{\alpha}$, $\hat{E}^*$, $\hat{C}^*$, and $\hat{\rho}$ are lower for the two years with trip limits, while the value of $\hat{\beta}$ is higher.

Values of the transformation parameters α and β reflect skewness¹ in the data. Positive or negative skewness is indi-

¹Pearson skewness (e.g. Kendall et al. 1987, p. 106) is positive if the mean exceeds the mode. Sokal and Rohlf (1969, p. 113) refer to this condition as right skewness because extreme outliers occur at the high (right) end of the distribution.

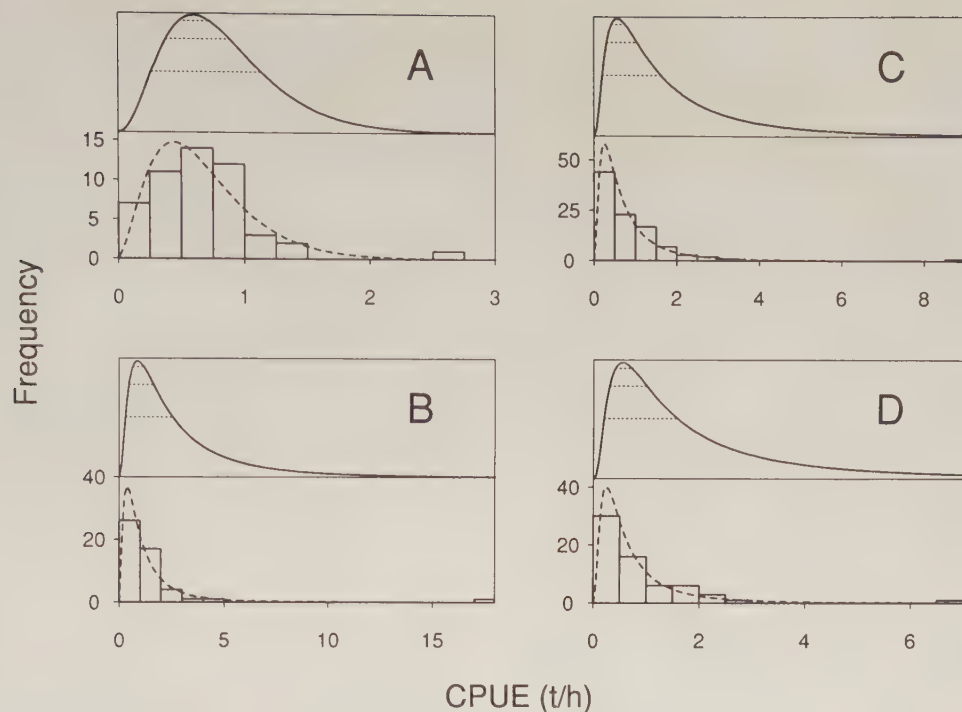


FIG. 1. Frequency histograms of the CPUE data I_i for (A) 1977, (B) 1980, (C) 1987, and (D) 1989. The dashed curve over the histogram represents the pdf [1.4], evaluated at the univariate parameter estimates (Table 6) and scaled to frequency by the product of n and the histogram bar width. The upper panel gives the corresponding pdf [1.3] on an arbitrary vertical scale, back-transformed to the variate I by (4.1). From top to bottom, respectively, the horizontal dotted lines represent the following percentiles for the pdf [1.3]: 25, 50, and 75%. Thus, 75% of the observations theoretically occur within the interval spanned by the bottom dotted line.

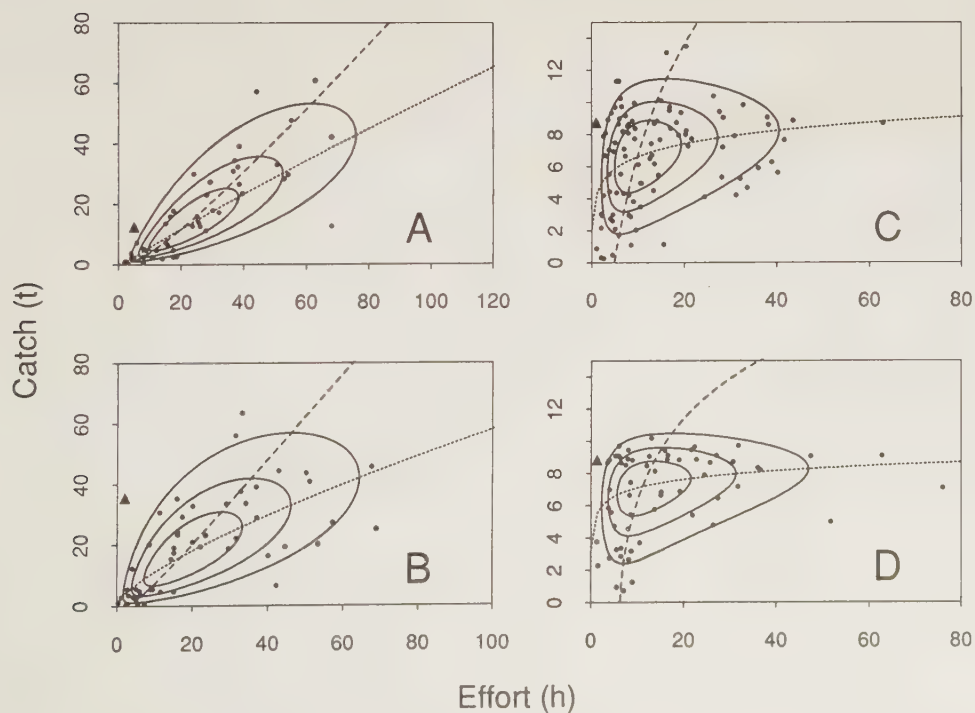


FIG. 2. Scatter plots of catch-effort data (E_i, C_i) for (A) 1977, (B) 1980, (C) 1987, and (D) 1989. The triangle in each panel identifies the outlying histogram bar in the corresponding panel of Fig. 1. The contours represent 25, 50, and 75% percentiles of the pdf [1.5], evaluated at the bivariate model estimates (Table 6). The dashed lines are defined by (1.10) and the dotted lines by (1.11). The contours and lines were obtained for the variates ξ and η and back-transformed to (E, C)-space by (4.2)–(4.3).

TABLE 6. Maximum likelihood parameter estimates for the four data sets. These are obtained by minimizing the functions [5.3] and [5.6] and applying relationships [2.1]–[2.4] and (1.12)–(1.14). Specified parameters for the univariate model are $(u, U) = (0.1, 3)$ and for the bivariate model are $(u, U, v) = (10, 50, 10)$. The choice for V in the bivariate model depends on the trip limit (TL).

Year	n	TL	Univariate estimates				Bivariate estimates														
			$\hat{\alpha}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{I}^*$	V	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\mu}$	$\hat{v}$	$\hat{\rho}$	$\hat{\sigma}$	$\hat{\tau}$	$\hat{a}_0$	$\hat{a}_1$	$\hat{b}_0$	$\hat{b}_1$	$\hat{E}^*$	$\hat{C}^*$	$\hat{\lambda}^*$
1977	50	—	0.33	0.38	0.18	0.58	50	0.17	0.24	0.78	0.62	0.83	0.20	0.24	-0.14	0.98	0.17	0.70	20.0	11.8	0.59
1980	50	—	0.01	0.64	0.27	0.89	50	0.31	0.40	0.67	0.60	0.71	0.26	0.27	0.10	0.75	0.21	0.67	16.9	16.1	0.95
1987	98	9	-0.03	0.52	0.27	0.57	10	0.06	0.99	0.70	0.66	0.34	0.16	0.29	0.21	0.64	0.28	0.18	9.9	6.6	0.67
1989	63	9	-0.08	0.53	0.26	0.54	10	0.05	1.59	0.73	0.59	0.30	0.16	0.29	0.18	0.57	0.39	0.16	11.2	7.2	0.64

cated by an exponent less than or greater than 1, respectively. For the univariate model, the estimate $\hat{\alpha} = 0.33$ corresponds to Fig. 1A, the I -histogram with the least amount of positive skew; for the remaining histograms, $\hat{\alpha}$ is near 0 and the data are approximately lognormally distributed. Estimates $\hat{\alpha}$ for the bivariate model are similar to the univariate estimates. Indeed, the effort data in Fig. 2 are positively skewed, with extreme points corresponding to high effort levels. The C -distribution, however, depends on the trip limit. For Fig. 2A and 2B, the catch data are positively skewed and values $\hat{\beta}$ are similar to $\hat{\alpha}$. For Fig. 2C, the catch data are approximately normally distributed and $\hat{\beta}$ is near 1. For Fig. 2D, the catch data are negatively skewed, and $\hat{\beta}$ is greater than 1.

Model results can also be illustrated in transformation space. Histograms of the four univariate series $\xi = \{\xi_i\}_{i=1, \dots, n}$ have similar ranges (Fig. 3A–3D). The solid curve represents the pdf [1.3], evaluated at the estimates $(\hat{\mu}, \hat{\sigma})$, and appropriately scaled. The scaling involves multiplying each point on the curve [1.3] by the product of the sample size n and the histogram bar width. The three dotted lines are derived from the pdf and

denote the predicted percentiles, centered at the median, for 25, 50, and 75% of the data. The transformed data ξ conform reasonably to the predicted normal distribution.

In original I -space (Fig. 1), the pdf [1.3] corresponds to a skewed curve, obtained through the back-transformation

$$(4.1) \quad I = [\xi(U^\alpha - u^\alpha) + u^\alpha]^{\frac{1}{\alpha}}$$

and displayed on an arbitrary vertical scale. The mode of the back-transformed pdf [1.3] occurs at the estimate $\hat{I}^*$. The back-transformed pdf is not a true pdf because it excludes the partial derivative in [1.4]. It does, however, serve to define quantiles centered at the median; an interval that includes, for example, 75% of the ξ -values transforms back to an interval including 75% of the I -values.

The dashed curves in Fig. 1 represent the actual pdf [1.4] for the univariate model, evaluated at the estimates $\hat{\theta}$, and scaled by n and the histogram bar width. These curves conform closely to the I -data, as anticipated. The mode of the dashed curve has

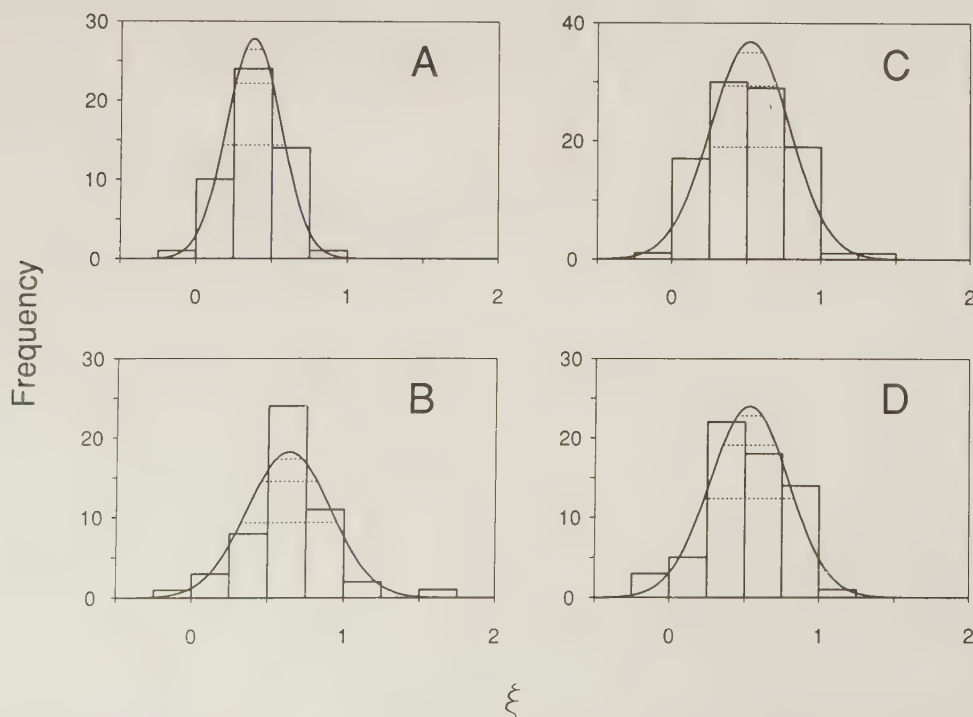


FIG. 3. Frequency histograms of the data ξ_i , obtained from I_i by (1.2), for (A) 1977, (B) 1980, (C) 1987, and (D) 1989. The solid curves correspond to the pdf [1.3], evaluated at the univariate parameter estimates (Table 6) and scaled to frequency by the product of n and the histogram bar width. From top to bottom, respectively, the horizontal dotted lines represent the following percentiles for the pdf [1.3]: 25, 50, and 75%.

no particular significance to our analysis, except that it should correspond approximately to the mode of the observed data.

Figures 2 and 4 illustrate the bivariate model. In (ξ, η) -space (Fig. 4), the four data sets occupy similar ranges. Contours of the pdf [1.5], evaluated at $(\hat{\mu}, \hat{\nu}, \hat{\sigma}, \hat{\tau})$, form concentric ellipses. The three contours indicate the regions predicted to include 25, 50, and 75% of the data. The data conform approximately to these predictions and are reasonably distributed within the regions. The two lines in each panel demonstrate the relationships (1.10)–(1.11); their intersection marks the point whose coordinates are medians (as well as means and modes) of the transformed bivariate distribution.

Following logic similar to that for the univariate model, the pdf [1.5] can be back-transformed (Fig. 2), based now on the two equations

$$(4.2) \quad E = [\xi(U^\alpha - u^\alpha) + u^\alpha]^{\frac{1}{\alpha}}$$

$$(4.3) \quad C = [\eta(V^\beta - v^\beta) + v^\beta]^{\frac{1}{\beta}}$$

In particular, the point $(\hat{\mu}, \hat{\nu})$ in Fig. 4 corresponds to $(\hat{E}^*, \hat{C}^*)$ in Fig. 2. The back-transformed contours become elongated and asymmetric, differences in contour shape between years with and without trip limits become pronounced, and the two lines in each panel become nonlinear. Incidentally, we have chosen not to illustrate the pdf [1.6] in Fig. 2. The contours of this function have similar shape to the curves shown here, except that they are skewed even closer to the origin. Note that the mode of the data, particularly in Fig. 2A and 2B, lies close to the origin.

The two curved lines in Fig. 2A–2D indicate the predicted median catch conditioned on effort, and conversely, the pre-

dicted median effort conditioned on catch. Catch–effort and effort–catch relationships appear similar for Fig. 2A and 2B, intercepting at low values (E_i, C_i) and increasing nearly linearly with catch or effort. Either catch or effort could be used as a predictor of the alternate variate. For Fig. 2C and 2D, however, median catch is nearly independent of effort at moderate to high values E_i . Furthermore, the variance in catch appears to decrease with increasing effort. Thus, under catch restrictions, it may be more meaningful to examine the level of effort required to achieve a given catch than to examine the level of catch obtainable from a given effort.

In practice, the most important model prediction is the estimate of CPUE and the confidence in that estimate. Approximate 95% confidence intervals for I^* and λ^* were determined from equations (2.4) and (2.9), respectively. The univariate estimate $\hat{I}^*$ is lower than the corresponding bivariate estimate $\hat{\lambda}^*$ for each of the data sets. The differences are not statistically meaningful, however, as the confidence intervals overlap considerably (Fig. 5). Confidence intervals for the bivariate model are slightly broader than the corresponding intervals for the univariate model. These broader intervals are probably more realistic, since they account for variability in the data pair (E_i, C_i) , rather than in the reduced data I_i .

To enable further comparisons between our models and standard methods, we also obtained the sample statistics $\bar{I}$, $\bar{I}^*$, $\bar{\lambda}$, and $\bar{\lambda}^*$. The median $\bar{I}^*$ is similar in value to $\hat{I}^*$ and $\hat{\lambda}^*$ for all four years. However, the statistics $\bar{I}$, $\bar{\lambda}$, and $\bar{\lambda}^*$ lead to CPUE measures inconsistent with $\hat{I}^*$ or $\hat{\lambda}^*$ for three of the years (Fig. 5). All of the statistics have similar values for 1977, the year for which the data are the least skewed. For the remaining years, $\bar{I}$ gives a CPUE estimate well above the model's 95% confidence intervals, reflecting a mean that is larger than the

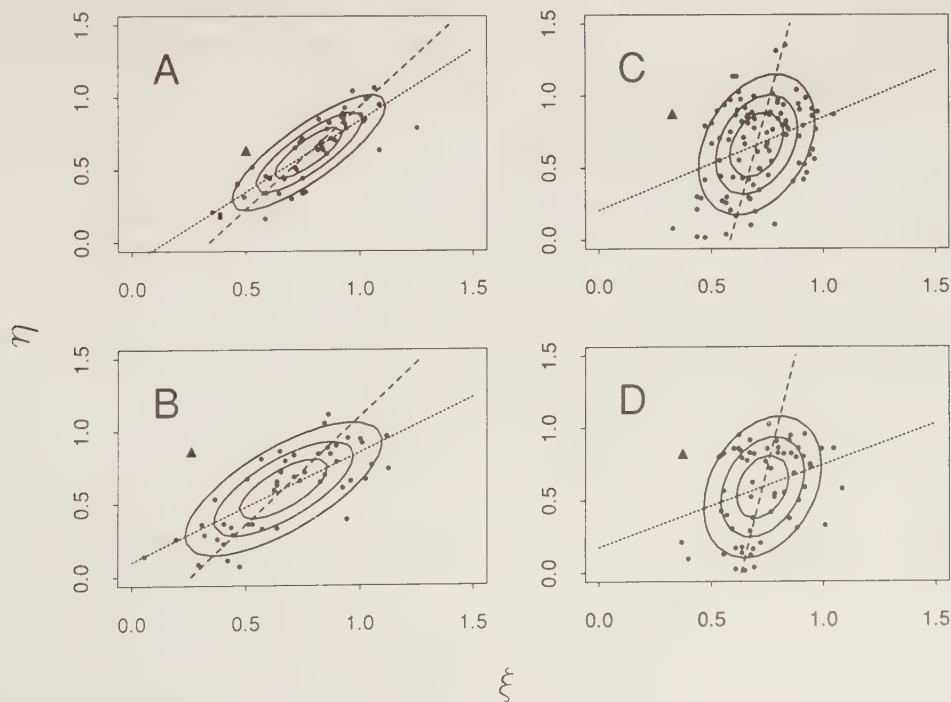


FIG. 4. Scatter plots of the data (ξ_i, η_i) , transformed from (E_i, C_i) by (1.2)–(1.3), for (A) 1977, (B) 1980, (C) 1987, and (D) 1989. The triangle in each panel identifies the outlying histogram bar in the corresponding panel of Fig. 1. The concentric ellipses represent 25, 50, and 75% percentiles of the pdf [1.5], evaluated at the bivariate model estimates (Table 6). The dashed lines are defined by (1.10) and the dotted lines by (1.11).

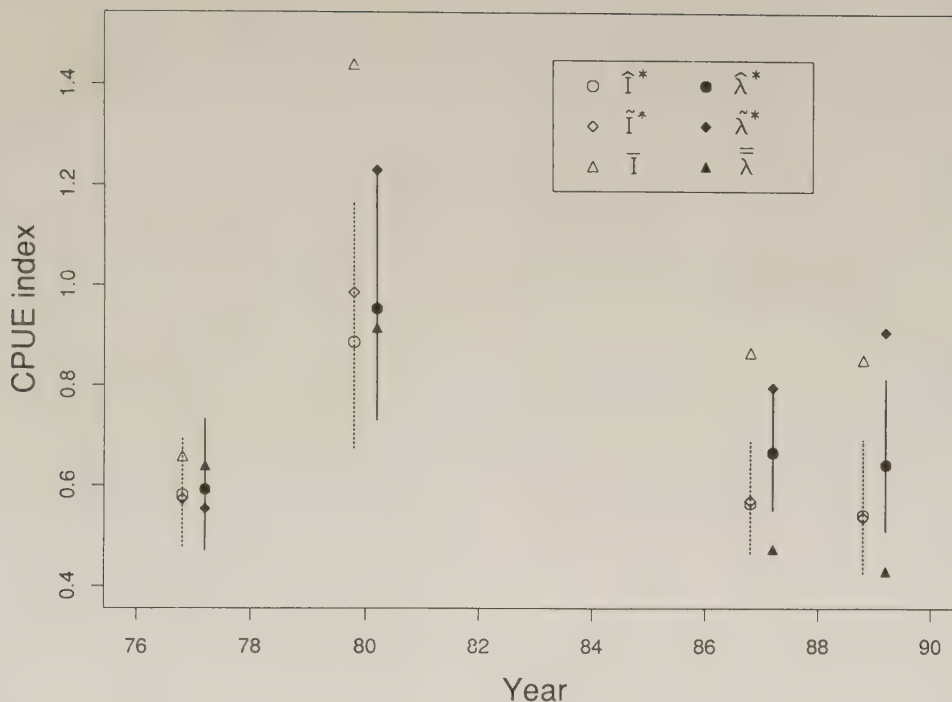


FIG. 5. Estimates and approximate 95% confidence intervals for $\hat{I}^*$ and $\hat{\lambda}^*$ and the corresponding sample statistics $\tilde{I}^*$, $\tilde{I}$, $\tilde{\lambda}^*$, $\bar{\lambda}$ for the four years of data.

median with positively skewed data. Values of the statistics $\tilde{\lambda}^*$ and $\bar{\lambda}$ are more difficult to interpret, since they are based on ratios. The common measure $\tilde{\lambda}^*$ and $\bar{\lambda}$ results in low estimates of CPUE for 1987 and 1989, the two years with a 9-t trip limit. This can be accounted for by negative skewness in the catch data and positive skewness in the effort data, so that mean effort is large relative to mean catch.

Our formulation allows us to examine model sensitivity to the value of the transformation parameters. For example, Quinn (1985) based his univariate analysis on $\alpha = 0.5$. Confidence in α for the univariate model is illustrated by the V-shaped curves in Fig. 6. Each curve represents the α -confidence interval from (2.5), where the vertical axis indicates the associated probability level. For example, the two points where the left and right branches of a curve meet the dotted line at probability 0.95 determine a 95% confidence interval for α . The curve minimum, with a probability level of 0, corresponds to $\alpha = \hat{\alpha}$. The value $\alpha = 0.5$ is exterior to the 95% confidence interval for all but one of the four data sets (1977).

Confidence in $(\hat{\alpha}, \hat{\beta})$ for the bivariate model can be examined using (2.10). Differences in $(\hat{\alpha}, \hat{\beta})$ are significant between years with and without trip limits (Fig. 7), since approximate 95% confidence regions for (α, β) are disjoint for the two sets of years. Confidence regions partially overlap for years within a management regime. The dotted line in Fig. 7 represents the hypothesis that $\alpha = \beta$. This hypothesis cannot be rejected for the two years without trip limits, but can be rejected easily for the two years with trip limits. These differences reflect skewness in the data (E_i, C_i) , as discussed above. Thus, it is not adequate to assume one transformation exponent for both catch and effort variates. In particular, the point $\alpha = \beta = 0.5$ lies within the confidence region for only one of the data sets (1980) and the point $\alpha = \beta = 0$ is external to all regions.

5. Discussion

Within the literature on CPUE estimation, our work is most closely related to Quinn's (1985) CPUE model for Pacific hal-

ibut (*Hippoglossus stenolepis*). The halibut model is clearly inadequate for rockfish CPUE data, however. Quinn (1985) selected a value of 0.5 for his transformation parameters. For the univariate model, the value $\alpha = 0.5$ lies within the 95% α -confidence interval for the 1977 data set only (Fig. 6). For the bivariate model, the values $\alpha = \beta = 0.5$ lie within the 95% (α, β) -confidence region for the 1980 data set only (Fig. 7). Furthermore, no values $\alpha = \beta$ are adequate for all four data sets. Quinn (1985) also showed that the variance in transformed halibut catch increased in proportion to transformed effort. We have already demonstrated (Fig. 2) that the variance in rockfish catch decreases with effort under trip limits. Since α and β are not constrained in our model, the transformations (1.2)–(1.3) produce homoscedastic variances in transformation space, while variances in the original space are adjusted automatically to conform to the data. Thus, additional ad hoc variance assumptions are unnecessary.

Of our two models, the univariate model has the advantage of simplicity, requiring only three parameters. In addition, the sample median $\tilde{I}^*$ provides a good approximation to the maximum likelihood estimate $\hat{I}^*$ for our examples. The price of this simplicity, however, is loss of information. We recommend use of the bivariate model over the univariate model, since it more fully accounts for the bivariate data structure. The bivariate model also offers flexibility in the selection of an abundance index. For example, an index might be defined as the median effort required to achieve a specified catch, or alternatively, the median catch required to achieve a specified effort. Such indices are estimable because of the relationships (1.10)–(1.11). With reparameterization as in (1.16), the new index could be included in the vector Φ , and confidence intervals for the index could be obtained.

Stock assessments typically involve comparisons among abundance indices in order to detect changes in abundance. For example, the bivariate model could be used to compute esti-

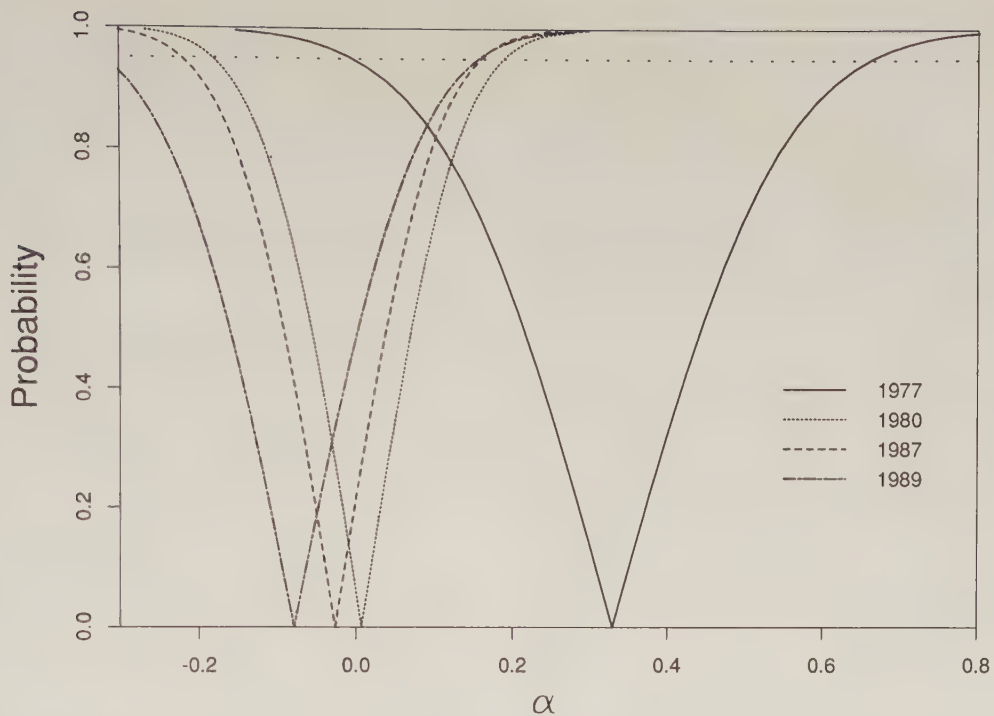


FIG. 6. Probability level from (2.5) associated with rejecting a given value of α for each data set. The horizontal dotted line corresponds to probability 0.95. The value of α at the intersection of the curve with the dotted line represents one endpoint of the 95% confidence interval.

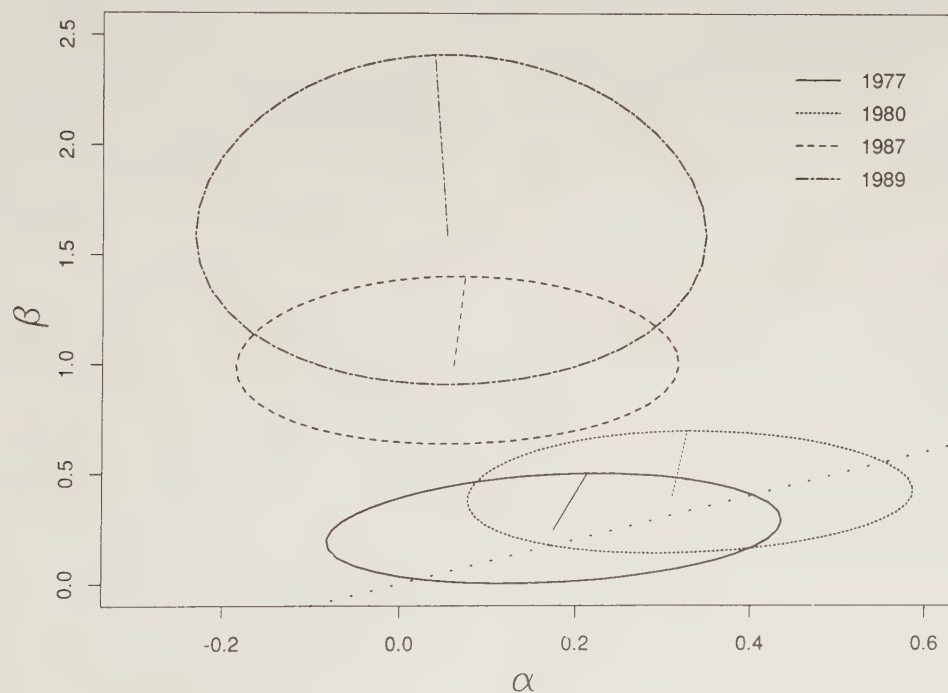


FIG. 7. Approximate 95% confidence regions for (α, β) from (2.10) for each of the data sets. The slanted lines join the estimates $(\hat{\alpha}, \hat{\beta})$ to the boundary of the corresponding region. The widely dotted line is the 45° line, where $\alpha = \beta$.

mates and confidence intervals for the selected index for each of several years under a similar management regime. Non-overlapping confidence intervals would be indicative of changes in stock abundance. A more rigorous approach would require modifications to the likelihood function to accommodate several data sets simultaneously. Such an analysis would have features in common with ANOVA and regression and could be

formulated entirely within the likelihood framework discussed here.

When the management regime changes, as with the imposition of trip limits, the biological interpretation of an abundance index may also change. The similarity in our estimates of $\hat{\lambda}^*$ between years with and without trip limits does not necessarily imply a similarity in stock abundance. To determine

the impact of management on $\hat{\lambda}^*$, a calibration period would be required during which both management regimes were in effect. For example, alternate weeks in the fishery could operate with and without trip limits. Calibration could also be used to relate different indices under similar or different conditions. For example, the median effort required to obtain a specified catch may be selected as the abundance index under trip limits, while the index $\hat{\lambda}^*$ may be selected under unrestricted fishing. Errors-in-variables methods are available for determining the relationship between different abundance indices (Richards and Schnute 1986; Richards 1987; Schnute et al. 1990), where the relationship may be nonlinear.

Data selection and standardization have long been important problems in the analysis of catch and effort data (e.g. Gulland 1956). For example, Kimura (1981) showed that gross vessel tonnage, the presence of echo sounders, and the type of trawl gear affected the CPUE of vessels fishing one British Columbia stock of Pacific ocean perch. One method of standardization would be to compute an abundance index for each set of conditions, for example, each class of vessels in the fishery. As discussed above, the relationship between any two indices could be determined by errors-in-variables methods, provided that calibration data are available. Alternatively, indices computed from independent data sets can be accommodated directly in modern catch-age analyses (Methot 1989, 1990).

Even when indices are calibrated and standardized, other types of biases could overwhelm any of the improvements suggested here. For example, the relationship between an abundance index and absolute abundance may be highly nonlinear (Peterman and Steer 1981; Bannerot and Austin 1983; Richards and Schnute 1986). Since different indices may relate differently to abundance, some indices may be more informative than others. An index with a highly asymptotic relationship to abundance would be a poor choice, since large changes in abundance might not be detected. Our bivariate methods provide a unified framework for investigating several alternative indices generated from the same catch and effort data set.

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Appendix

This appendix presents exact likelihood functions for the univariate and bivariate models, taking account of the truncations discussed in the last paragraph of section 2. Consider first the univariate model (1.2) and (1.4) with $\alpha > 0$. In this case, positive values of x correspond to values of ξ in the range (c_ξ, ∞) . Define

$$(A.1) \quad T_1(\mu, \sigma, c_\xi) = \int_{c_\xi}^{\infty} p(\xi|\mu, \sigma) d\xi$$

and

$$(A.2) \quad p_T(\xi|\mu, \sigma, c_\xi) = \frac{p(\xi|\mu, \sigma)}{T_1(\mu, \sigma, c_\xi)}.$$

Then $p_T(\xi)$ defines a pdf for ξ over the truncated range, since

$$\int_{c_\xi}^{\infty} p_T(\xi) d\xi = 1.$$

It follows that

$$(A.3) \quad p_T(x|\alpha, \mu, \sigma) = p_T(\xi(x)|\mu, \sigma, c_\xi(\alpha)) \frac{\partial \xi(x, \alpha)}{\partial x}$$

is an exact pdf for x on the range $(0, \infty)$. In the right side of (A.3), we emphasize dependencies on all parameters, particularly α .

Comparing (A.3) with [1.4] shows that the exact and approximate pdf for x agree, except that the exact pdf includes the extra factor $1/T_1(\mu, \sigma, c_\xi(\alpha))$. This adjustment corrects for the loss of probability associated with values of ξ outside the admissible range. The exact likelihood $P_T(\mathbf{x}|\boldsymbol{\theta})$ for the univariate model is thus given by a version of (2.1) in which $p(x_i|\boldsymbol{\theta})$ is replaced by the exact pdf (A.3) for x_i . Consequently, from (2.2) the exact value $K_T(\boldsymbol{\theta})$ is

$$(A.4) \quad K_T(\boldsymbol{\theta}) = K(\boldsymbol{\theta}) + 2n \ln [T_1(\mu, \sigma, c_\xi(\alpha))],$$

where $K(\boldsymbol{\theta})$ denotes the approximation [5.3]. The correction term in (A.4) involves the quantity T_1 , which depends only on the parameter vector $\boldsymbol{\theta} = (\alpha, \mu, \sigma)$.

When $\alpha > 0$, equations (A.1) and (A.4) give an exact version of the univariate inference function defined in (2.2). A similar result applies when $\alpha < 0$, except that the range of integration in (A.1) becomes $(-\infty, c_\xi)$. In the special case

$\alpha = 0$, the integration range is $(-\infty, \infty)$; thus, $T_1 = 1$ and [5.3] is exact for the lognormal distribution.

The exact bivariate likelihood can be obtained in a manner analogous to that for the univariate model. When $\alpha > 0$ and $\beta > 0$, define

$$(A.5) \quad T_2(\mu, \nu, \rho, \sigma, \tau, c_\xi, c_\eta) = \int_{c_\xi}^{\infty} \int_{c_\eta}^{\infty} q(\xi, \eta|\mu, \nu, \rho, \sigma, \tau) d\xi d\eta.$$

Then it can be proved that the exact inference function $L_T(\boldsymbol{\Phi})$ for the bivariate model is

$$(A.6) \quad L_T(\boldsymbol{\Phi}) = L(\boldsymbol{\Phi}) + 2n \ln [T_2(\mu, \nu, \rho, \sigma, \tau, c_\xi(\alpha), c_\eta(\beta))],$$

where $L(\boldsymbol{\Phi})$ denotes the approximation [5.6]. Here the correction term involves the quantity T_2 , which depends only on the parameter vector $\boldsymbol{\Phi} = (\alpha, \beta, \mu, \nu, \rho, \sigma, \tau)$. Similar results apply when $\alpha < 0$ and/or $\beta < 0$, except that the two integration ranges in (A.5) must be altered in a manner analogous to that discussed for the univariate model.

The exact functions $K_T(\boldsymbol{\theta})$ and $L_T(\boldsymbol{\Phi})$ depend on their parameters in a more complex fashion than the approximations $K(\boldsymbol{\theta})$ and $L(\boldsymbol{\Phi})$. Consequently, given the definitions in Table 3, exact analytical results analogous to those in Table 5 are not possible. All analyses proposed here could be based on exact likelihood functions; however, the numerical minimizations in Table 3 would require increased computing time.

We recommend an analysis based on the approximations in the body of this paper. When the analysis is complete for a given data set and model, the corresponding value T_1 or T_2 can be computed. If this value is very close to 1, as it usually is, then the approximation is justified. In the examples presented here, values of T_1 and T_2 lie in the interval $(1-10^{-6}, 1)$, and the corrections in (A.4) and (A.6) have a negligible effect on our results.

Radioisotope Method for Estimating Food Consumption by Brown Trout (*Salmo trutta*)

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A fast, simple, and reliable method for estimating food consumption using radioisotopes is presented. The method gives both sensitive short-term and robust long-term estimates of food consumption for brown trout (*Salmo trutta*). The estimates of daily food rations were similar to those estimated from rates of gastric evacuation and laboratory experiments. The radioisotope method can be used to detect variations in ration size due to temperature, fish size, and food availability. Information on radiocesium absorption from this study and earlier published data on radiocesium retention can be used to estimate daily ration for both piscivorous and benthivorous brown trout. The radioisotope method can be used in radiocesium-contaminated lakes, but it could also be used in other experimental situations by adding stable cesium to small water bodies. The same method is also applicable for use with other stable or radioactive isotopes.

On présente une méthode rapide, simple et fiable pour estimer la consommation de nourriture à l'aide de radioisotopes. Cette méthode donne des estimations sensibles à court terme et des estimations robustes à long terme de la quantité de nourriture que consomme la truite brune (*Salmo trutta*). Ainsi, les estimations des rations quotidiennes étaient semblables à celles établies à partir de taux d'évacuation gastrique et d'expériences en laboratoire. La méthode basée sur des radio-isotopes peut être utilisée pour identifier des variations de la ration dues à la température, la taille du poisson et la disponibilité de nourriture. L'information sur l'absorption du césium radioactif recueillie au cours de cette expérience et les données déjà publiées sur sa rétention peuvent être utilisées pour déterminer la ration quotidienne de truites brunes piscivores et benthivores. La méthode des radio-isotopes peut être utilisée dans des lacs contaminés de césium radioactif, bien qu'elle peut aussi être utilisée dans le cadre d'autres expériences si l'on ajoute du césium stable à de petits plans d'eau. Cette méthode peut aussi être appliquée à d'autres isotopes stables ou radioactifs.

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By estimating food consumption, we assess the demands that fish make on their food resources and how food limits survival, growth, and reproduction of the animals (Wootton 1990). Estimates of food consumption in natural fish populations are often based on measurements of gut fullness and the rate of food passage through the gut. Elliott and Persson (1978) described a method for estimating the consumption rate of wild fish based on laboratory measurements of gastric evacuation rate and measurements of the amounts of food in the stomachs of fish sampled at the beginning and end of the period studied. A simpler method for estimating daily food consumption (D) was given by Eggers (1977):

$$(1) \quad D = 24 FR$$

where F is mean weight of gut contents during the period and R is the rate of gastric evacuation. Field studies (Allen and Wootton 1984; Boisclair and Leggett 1988) have demonstrated that the two methods give similar results. However, both the methods of Eggers (1977) and Elliott and Persson (1978) give

the consumption for 1 d only, and this estimate cannot be used for generalization if food consumption varies between days. An alternative way to obtain food consumption estimates covering longer time periods is to use bioenergetic mass balance equations. In this type of study, the consumption rate is estimated from the observed growth rate by making assumptions about the energy losses associated with metabolism and excretion (Winberg 1956; Paloheimo and Dickie 1966a, 1966b).

The methods of Elliott and Persson (1978) and Eggers (1977) for estimating daily consumption rates are time consuming, and there is need for development of simpler methods. Davis and Foster (1958) suggested an alternative method using a radioactive isotope in which the turnover rate of the isotope in the fish must be known. Advantages of the radioisotope method are that it is easy to use, sample analysis is rapid, and it may be used to estimate food consumption over prolonged periods of time. The radioisotope method has been used for estimating the food consumption of common carp (*Cyprinus carpio*) (Kevern 1966), bluegill (*Lepomis macrochirus*) (Kolehmainen

1974), and rainbow trout (*Oncorhynchus mykiss*) (Hakonson et al. 1975), but the reliability of the method has not been tested.

This paper describes a radioisotope method for estimating food consumption of brown trout (*Salmo trutta*). Estimates obtained using this method were compared with estimates based on the Eggers (1977) method and results from laboratory studies which determined the food consumption by brown trout under different conditions (Elliott 1975a, 1975b, 1975c).

Methods

Study Area and Sampling

Fish were sampled in Høysjøen (area 1.0 km², maximum depth 26.5 m), a dysoligotrophic (Secchi disk transparency 2.2–3.3 m) dimictic lake situated 222 m above sea level in central Norway. The lake is ice-free from mid-May to early November. The lake and its watershed received about 50 kBq radiocesium·m⁻² (¹³⁴Cs and ¹³⁷Cs) as a result of the Chernobyl fallout 28 April 1986 (Forseth et al. 1991). The levels of radiocesium in fish from Høysjøen were high in 1986, and the removal of the isotopes has been slow (Forseth et al. 1991). The lake supports dense populations of brown trout and Arctic char (*Salvelinus alpinus*).

Brown trout were sampled by gillnetting (panel size 1.5 × 25 m, various mesh sizes including 12.5, 16, 19.5, 24, 29, and 35 mm) four times in 1987 (June, July, September, and October) and three times in both 1988 (June, August, and September) and 1989 (May, July, and October). The nets were set on bottom in the littoral zone (0–3 m). Throughout 1987 and May and July 1989, the nets were pulled every 4 h throughout one 24-h period. Supplementary fishing was then performed on the two following days to ensure that sufficient fish were sampled to enable estimation of food consumption by the Eggers (1977) method. On all other sampling days, the nets were pulled every 6 or 8 h, and fish captured on those instances were used to estimate food consumption by the radioisotope method only. A lower limit of 15 fishes from each age group on each sampling was considered adequate for making food consumption estimates by the radioisotope method. Each fish was weighed (grams), total length (millimetres) measured, deep frozen, and the age determined by use of sacculus otoliths and scales (Jonsson 1976). The stomachs were removed and frozen as soon as possible after the nets were pulled. In the laboratory, the proportion (by volume) of zooplankton, molluscs, surface insects, chironomid zoobenthos, and other zoobenthos was determined through analysis of stomach contents. The stomach contents were then dried (65°C for 48 h) and weighed. The radioactivity in each prey category was determined separately in 1987, while pooled samples were measured in 1988 and 1989. Fish muscle subsamples were prepared in the laboratory and radioactivity measured individually.

Radioisotope Method

The rate at which the radiocesium body burden (Q , becquerels) in fish changes with time (dQ/dt) is proportional to the intake rate (I , becquerels per day) minus the elimination rate (kQ):

$$(2) \quad \frac{dQ}{dt} = I - kQ$$

where k (per day) is an effective rate constant (physical decay of the isotope and excretion rate). Equation (2) can be inte-

grated assuming that I and k both are constant during the time period under consideration:

$$Q_t = Q_0 \cdot e^{-kt} + \frac{I}{k} (1 - e^{-kt})$$

where Q_0 and Q_t are ¹³⁷Cs body burdens (becquerels) in fish at times 0 and t , respectively, given by $Q = C_f W$ where C_f is radiocesium specific activity (becquerels per gram) and W is fish weight (grams). By rearranging the equation, we get

$$(3a) \quad I = \frac{Q_t - Q_0 e^{-kt}}{1 - e^{-kt}} \cdot k.$$

The integration of equation (2) is only truly valid if the excretion (k) and intake (I) are constant during the time period under consideration. However, excretion is a function of both fish weight and ambient temperature (Hewett and Jefferies 1976), and intake may be expected to vary with season. Equation (3a) was therefore calculated in a stepwise fashion, with separate variable values for each successive day. Then $Q_0 = Q_i$ and $Q_t = Q_{i+1}$, where i is 1 d ($t = 1$ d). Both k and I were assumed to be constant during this short period. Equation (3a) can now be written as

$$(3b) \quad I_i = \frac{Q_{i+1} - Q_i e^{-k_i}}{1 - e^{-k_i}} \cdot k_i.$$

The daily ration D_i can be calculated by dividing the daily radiocesium intake by the radiocesium concentration that is absorbed by brown trout from its prey:

$$(4) \quad D_i = \frac{I_i}{\sum_j b_{ij} \cdot C_{pij} \cdot f_{ij}}$$

where b_{ij} is the absorption of radiocesium from the j th prey item, C_{pij} is the radioactivity in the j th prey item (becquerels per gram), and f_{ij} is the proportion by volume of the j th prey item in the diet of brown trout (Kevern 1966; Kolehmainen 1974).

¹³⁷Cs has a physical half-life of approximately 30 yr, and consequently, for the purposes of the present study, physical decay was ignored. Two different methods were used to estimate daily values. In the first, the short-term method, daily values were calculated from a linear interpolation between the values determined for subsequent sampling dates. The year-classes 1+ to 4+ were used in these computations, and average daily rations for brown trout were estimated in periods between two sampling dates. In the other, the long-term method, daily rations for brown trout that hatched in spring 1986 were monitored from June 1988 (age 2+) to October 1989 (age 3+). Daily values of the variables in equations (3b) and (4) were derived from curve fits to available data for fish and prey radioactivity, ambient temperature, and fish weight. This method produced daily ration estimates and was used in a long-term development study, taking temperature, season, and growth rates into consideration.

Radiocesium Retention

The retention of radiocesium in fish depends on the duration and frequency of the isotope intake. Fish that receive an acute oral radiocesium dose generally show two-component retention curves (Kevern 1966; Gallegos and Whicker 1971). Short-lived components represent unassimilated material and the proportion of assimilated radiocesium that is rapidly excreted.

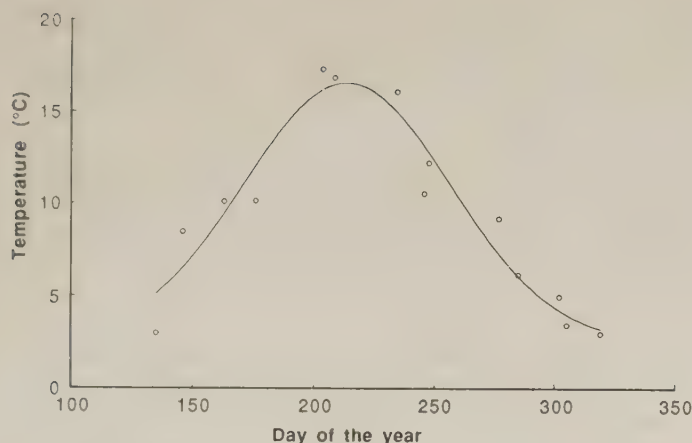


FIG. 1. Gaussian curve fit to pooled temperature observations in Lake Høysjøen, 1987–89 ($R^2 = 0.92$). Day number 1 is 1 January.

The quantitatively more important long-lived component represents assimilated material, and the major residence time of radiocesium is determined by this component (Reichle et al. 1970; Mailhot et al. 1989). Under conditions of a continuous intake of contaminated food, the importance of short-lived components decreases (Kolehmainen 1974). The studies that report radiocesium retention by brown trout (Hewett and Jeffries 1976; Ugedal et al. 1992) primarily deal with the long-lived component. The fast rate of excretion was excluded from the computations.

Radiocesium retention in fish is influenced by factors such as ambient temperature and body weight. The slow rate constant of radiocesium excretion (k) was computed for each day, taking daily ambient temperature (T , degrees Celsius) and fish weight (W , grams) into consideration (Ugedal et al. 1992):

$$(5) \quad t_{1/2} = 290W^{0.176}e^{-0.106T}$$

and

$$(6) \quad k = \frac{\ln 2}{t_{1/2}}$$

where $t_{1/2}$ is the biological half-life of radiocesium. A general temperature curve for 1988 and 1989 was developed by plotting grouped temperature observations from 1987 to 1989. Mean temperature of the 0–3 m depth zone, where most brown trout live (Forseth et al. 1991), was used. The observations fitted well to the Gaussian curve (Fig. 1):

$$(7) \quad y = a + b \cdot e^{-(x-c)^2/d^2}$$

where y is the temperature (degrees Celsius) and x is the number of days after 1 January. Model (7) is symmetrical around a maximum value. Temperature in temperate lakes, however, is known to increase rapidly during spring and decrease slowly during autumn. To simulate this skewed distribution, a Gaussian curve fit was performed on logarithmic transformed day numbers ($\ln x$). This model was used in a least square error curve fit to the observed temperatures in the lake in 1988 and 1989 separately. As the numbers of observations for each year were low, two parameters were treated as constants. The base-line (a in equation (7)) was set at 2°C, which is the assumed winter temperature for brown trout in the lake based on temperature registration taken during early March 1987. Furthermore, the day number at which the temperature was at its

maximum each year was treated as a constant. This warmest day each year was determined by comparing temperature registrations taken in water with those taken in air at the nearest meteorological station (situated approximately 30 km from Lake Høysjøen).

Radiocesium Absorption

The absorption of radiocesium in brown trout is defined by the long-lived component for excretion of radiocesium administered to the fish. The absorption of ^{134}Cs by brown trout from different food items (Ephemeroptera sp. larvae, *Gammarus lacustris*, freshwater gastropods, Chironomidae sp. larvae, zooplankton, and brown trout muscle) was studied in feeding experiments. Live prey were sampled at different locations and kept in an aquarium in a solution of ^{134}Cs (1.5–2.5 L, 1–2 kBq·mL⁻¹) until sufficient radioactivity was recorded ($>1.5 \text{ kBq} \cdot \text{g}^{-1}$) in the prey organisms. Subsamples of the prey (0.1–0.3 g) were washed twice in distilled water and once in ethanol (96%), radioactivity was measured, and prey were then transferred to 1-mL disposable plastic syringes filled with a solution of gelatine in water. When the gelatine solution set, the prey were surrounded by gelatine. This facilitated administration of portion of prey to the brown trout and prevented loss of material. Radiocesium-contaminated fish muscle was obtained by administering a radioactive gelatine jelly (20–40 kBq) to brown trout (100–150 g). When feeding the brown trout, the syringes were introduced into the esophagus and the gel forced into the stomach of the fish. After 2 d, fish were slaughtered and muscle samples (0.5 g) were prepared for use in the feeding experiments.

Brown trout (live weight 250–450 g) used in the feeding experiments were anaesthetized with chlorobutanol and tagged with a numbered Carlin tag (Carlin 1955). The labelled prey (0.1–0.3 g, 200–7000 Bq) was forced into the stomach of the fish by the procedure described above. Ten fish were tested for each of the prey groups. The fish were kept in 4-m² hatchery tanks with continuous water flow at a temperature of 14°C and fed commercial pellets (EWOS) to satiation. After 10 d, ^{134}Cs excreted by the short-lived component comprised less than 5% of total added radioactivity (Ugedal et al. 1992), and the fish were slaughtered, weighed, and deep frozen. Prior to counting radioactivity, the fish were cut into pieces, dried (96°C for 48 h), homogenized, and a 10-g sample taken.

The absorption factor (b_j) from each prey type (j) was

$$(8) \quad b_j = \frac{A_f}{A_p}$$

where A_f (counts per second per fish) represents the radiocesium body burden of fish and A_p (counts per second) is the radioactivity administered to the fish.

Radiocesium measurements were based on integral gamma ray counting above a threshold of 125 keV with a Harshaw integral line scintillation detector (type 12SW12-W4) with a 75·75-mm ø NaI well crystal and a 25 mm ø cylindrical well.

When estimates of food consumption were made, it was assumed that values obtained for Ephemeroptera larvae and *G. lacustris* were representative for both surface insects and zoobenthos, that values for freshwater gastropods could be used for all molluscs, and that values for Chironomidae larvae were representative for chironomid zoobenthos (both larvae and pupae).

TABLE 1. Mean relative (weight-specific) daily rations (mg dw·g fw⁻¹) for different aged brown trout at different times, and total food consumption throughout each season, estimated by the short-term radioisotope method. The method gave negative estimates (–) in some cases.

Date	Year	Temperature (°C)	Age (yr)				
			1+	2+	3+	2+ and 3+	2+ to 3+
21 July to 2 Sept.	1987	13.7				8.27	
2 Sept. to 27 Oct.	1987	7.8				1.19	
Summer	1987					402.6	
27 Oct. to 14 June	1987–88	3					0.86
14 June to 11 Aug.	1988	13.2		9.36	4.14	6.19	
11 Aug. to 22 Sept.	1988	12.7		5.02	20.67	11.49	
Summer	1988			754.4	1109.1	842.9	
22 Sept. to 25 May	1988–89	3					1.75
25 May to 27 July	1989	12.7		15.00	10.15	10.46	
27 July to 11 Oct.	1989	11.5	4.39	–	–	–	
Summer	1989			945.4	639.6	659.0	

Results

Radioisotope Method

Percent absorption of radiocesium ($\pm$ SE) by brown trout was estimated to be as follows: Chironomidae sp. larvae, 54.8 (5.2); *G. lacustris*, 48.0 (5.3); freshwater snails, 75.9 (3.6); Ephemeroptera sp. larvae, 23.4 (2.3); zooplankton, 81.6 (4.4); brown trout muscle, 65.9 (1.0). Radiocesium absorption thus differed among food items, with brown trout exhibiting highest absorption from zooplankton and lowest from Ephemeroptera larvae.

Mean relative (weight-specific) daily rations, estimated by the short-term radioisotope method, varied within each season, among years, and between age groups (Table 1). Rations were generally large in midsummer, smaller in autumn, and smallest in winter. The estimated weight-specific food consumption during each season was similar. The relation between daily ration (D , milligrams dry weight), fish weight (W , grams), and temperature (T , degrees Celsius) was described by the equation

$$\ln D = \ln a + b_1 \ln W + b_2 T$$

where a , b_1 , and b_2 are constants (Elliott 1975a). Parameters were estimated ($\pm$ SE) to be $\ln a = 0.371$, $b_1 = 0.773$ (0.374), and $b_2 = 0.199$ (0.039) ($R^2 = 0.69$, $F_{2,10} = 14.16$, $p = 0.0012$) for the temperature range 3.0–13.9°C. Daily rations were generally smaller than maximum rations estimated from laboratory studies (Elliott 1975a) for all weights and temperatures (Fig. 2). The rations from the present study and Elliott's laboratory studies did, however, vary in a similar way with fish size and ambient temperature.

The parameters needed for estimating food consumption by the long-term radioisotope method were computed using different curve fit equations. Weight (W , grams) of age 2+ brown trout on each day (d , day number after 14 June 1988) was estimated from

$$W = \frac{59.1}{1 + 0.778 \cdot 0.974^d}$$

for the period 14 June 1988 to 11 May 1989, and weight of age 3+ brown trout on each day (d , day number after 11 May 1989) from 12 May to 11 October 1989 was estimated from

$$W = 58.6 + \frac{43.1}{1 + 97.7 \cdot 0.918^d}$$

These equations were derived from a logistic trend (Neter et al.

1988) least square error curve fit to the observed weights. Two equations were derived because no single curve was found to be suitable for describing growth throughout the period. Good fits to the observed weights ($R^2 = 0.98$) were obtained.

A function of the type $y = ae^{-bx}$ was fitted to the observed radioactivity in brown trout, and the specific activity (C_f , becquerels per gram) at each day (d , day number after 28 April 1986) was computed by

$$C_f = 3540e^{-0.000545d}, \quad R^2 = 0.80.$$

The radioactivity in prey animals from brown trout stomachs (C_p , becquerels per gram) on each day (d , day number) was derived from a linear regression to the observed prey radioactivity:

$$C_p = 8700 - 3.600d, \quad R^2 = 0.36.$$

The diet of brown trout varied largely between samplings. No curves could therefore be fitted to the proportions of each prey category in the diets of the brown trout throughout 1988 and 1989. Daily values for percent contribution of each of the five prey categories in the stomach were therefore calculated by linear interpolations between proportions at consecutive samplings.

Temperature (T , degrees Celsius) in Lake Høysjøen on each day ($\ln d$, day number after 1 January 1988) in 1988 was estimated by the Gaussian fit as

$$T = 2.0 + 15.0 \cdot e^{-(d-6.71)^2/0.071^2}$$

and on each day ($\ln d$, day number after 1 January 1989) in 1989 as

$$T = 2.0 + 15.0 \cdot e^{-(d-7.07)^2/0.052^2}.$$

Highest daily rations for brown trout hatched in spring 1986 were found in June both in 1988 and 1989 (Fig. 3), and relative (weight-specific) ration (milligrams dry weight per gram fresh weight of fish) was slightly lower for age 3+ brown trout in 1989 than age 2+ brown trout in 1988. Absolute rations (milligrams dry weight) in 1989 were, however, generally larger than during the corresponding periods in 1988. The development in ration level through the observed period was in good accordance with the temperature development (Fig. 3). Rations were generally higher than maintenance rations and lower than the maximum rations estimated by Elliott (1975a, 1975b, 1975c) in laboratory studies. The rations estimated for brown trout in Høysjøen were, however, similar to or higher

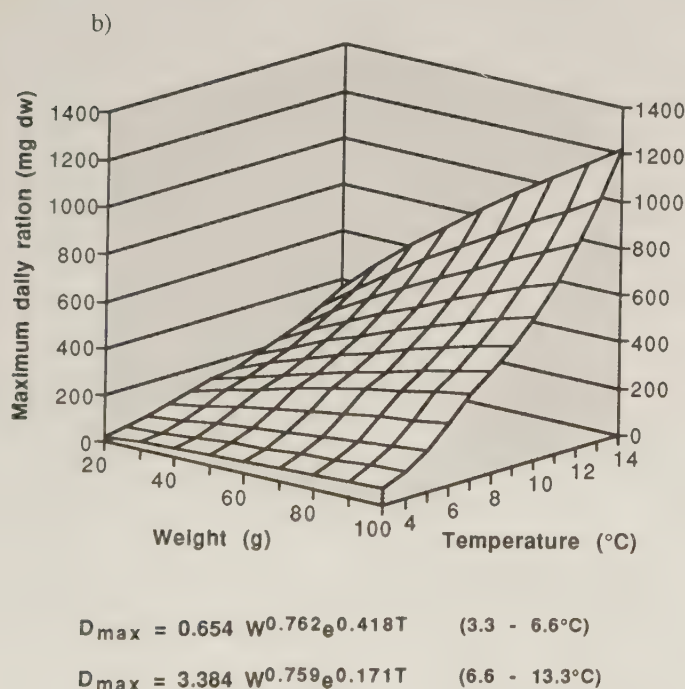
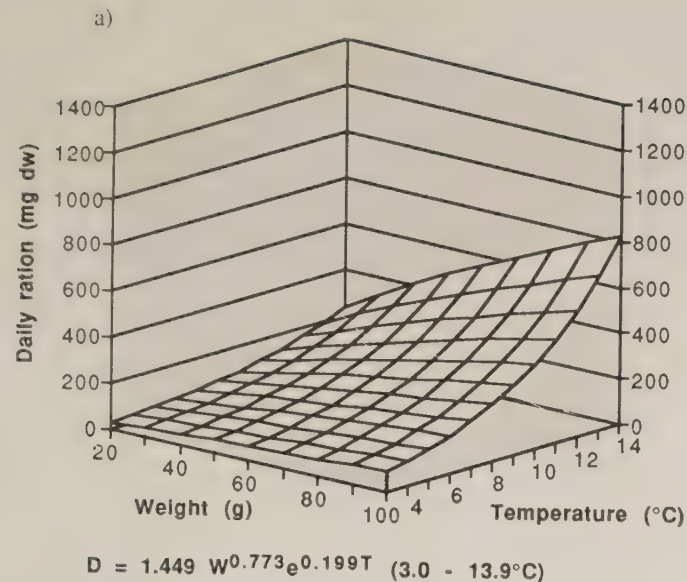


FIG. 2. Relation between (a) fish weight (W), ambient temperature (T), and daily ration (D) for brown trout from Lake Høysjøen, 1987–89 and (b) fish weight, ambient temperature, and maximum daily ration ($D_{\max}$) for brown trout estimated from laboratory experiments (Elliott 1975a).

than the laboratory-determined maximum rations during early summer.

Food consumption estimates obtained with the long-term radioisotope method were similar to those obtained with the short-term method. Food consumption (milligrams dry weight per gram fresh weight) estimated by the long-term method were 550 from June to August and 205 from August to September for age 2+ brown trout in 1988 and 540 for age 3+ brown trout from May to July 1989. Corresponding short-term estimates were 540, 210, and 640, respectively.

Eggers (1977) Method

Brown trout daily rations (D , milligrams dry weight per gram fresh weight) estimated by the Eggers (1977) method (equation (1)) with information on brown trout evacuation rate from Elliott (1972) were high in June and July 1987 and then decreased at the end of the season (Table 2). The estimates were also high in May and July 1989 and were similar to those in 1987.

The radioisotope and Eggers methods gave similar estimates of daily rations from July to October 1987 (Table 3). The estimates for food consumption 1989 were also similar. The general pattern was for a high ration in early summer, decreasing towards autumn (Fig. 4).

Discussion

To evaluate the radioisotope method for estimating brown trout food consumption, we have compared values obtained with ration sizes estimated by the Eggers (1977) method. The estimates of food consumption obtained using the two methods were almost identical, which suggests that the radioisotope method is robust and reliable.

In general, the estimated rations obtained for brown trout in Høysjøen lay between maximum and maintenance rations determined in laboratory studies (Elliott 1975a, 1975b, 1975c). There were, however, discrepancies with expectations on two occasions. The rations for age 2+ brown trout in early summer 1988 and for age 3+ fish in early spring 1989 were equal to or higher than maximum rations estimated from laboratory studies by Elliott (1975a, 1975b). Several experimental studies (e.g. Weatherley and Gill 1981; Dobson and Holmes 1984; Miglavs and Jobling 1989) with salmonid species have revealed that following a period of starvation or food deprivation, fish enter a period of high growth, termed recovery growth. Such growth probably occurs as a result of a hyperphagic response and higher efficiency in food utilization (Miglavs and Jobling 1989). Thus, the fact that our estimates for daily rations were equal to or exceeded laboratory estimates for the maximum rations does not negate the validity of these estimates, since high rates of consumption would be expected after long periods of food deprivation (rations at maintenance level) during winter. We thus conclude that the radioisotope method is reliable because it gives estimates in accordance with other methods and expectations from laboratory studies.

The radioisotope method for estimating fish food consumption can give both short-term estimates and robust long-term estimates. Short-term studies, where daily rations are estimated between two subsequent sampling dates, are appropriate for detecting small changes in ration levels. The method is, however, highly sensitive to erroneous estimates of different parameters in the computations, and extreme values have a large impact on the results. On some occasions in the current study, negative values for short-term food consumption were obtained. To avoid such effects, large numbers of fish should be sampled, with at least 20 fish of each age group being examined at each sampling. It is not possible to use the short-term method to study patterns of ration level over longer periods. To achieve estimates for longer periods, the alternative, less-sensitive, but more robust method can be used. This method, where the parameters needed for the estimates are derived from curve fit equations, is less sensitive to erroneous estimates of the parameters at each sampling date, and fewer fish need to be sampled.

Potential errors which may occur when using the radioisotope method are inaccurate estimates of radiocesium absorption and retention. In our case, the absorption experiment was

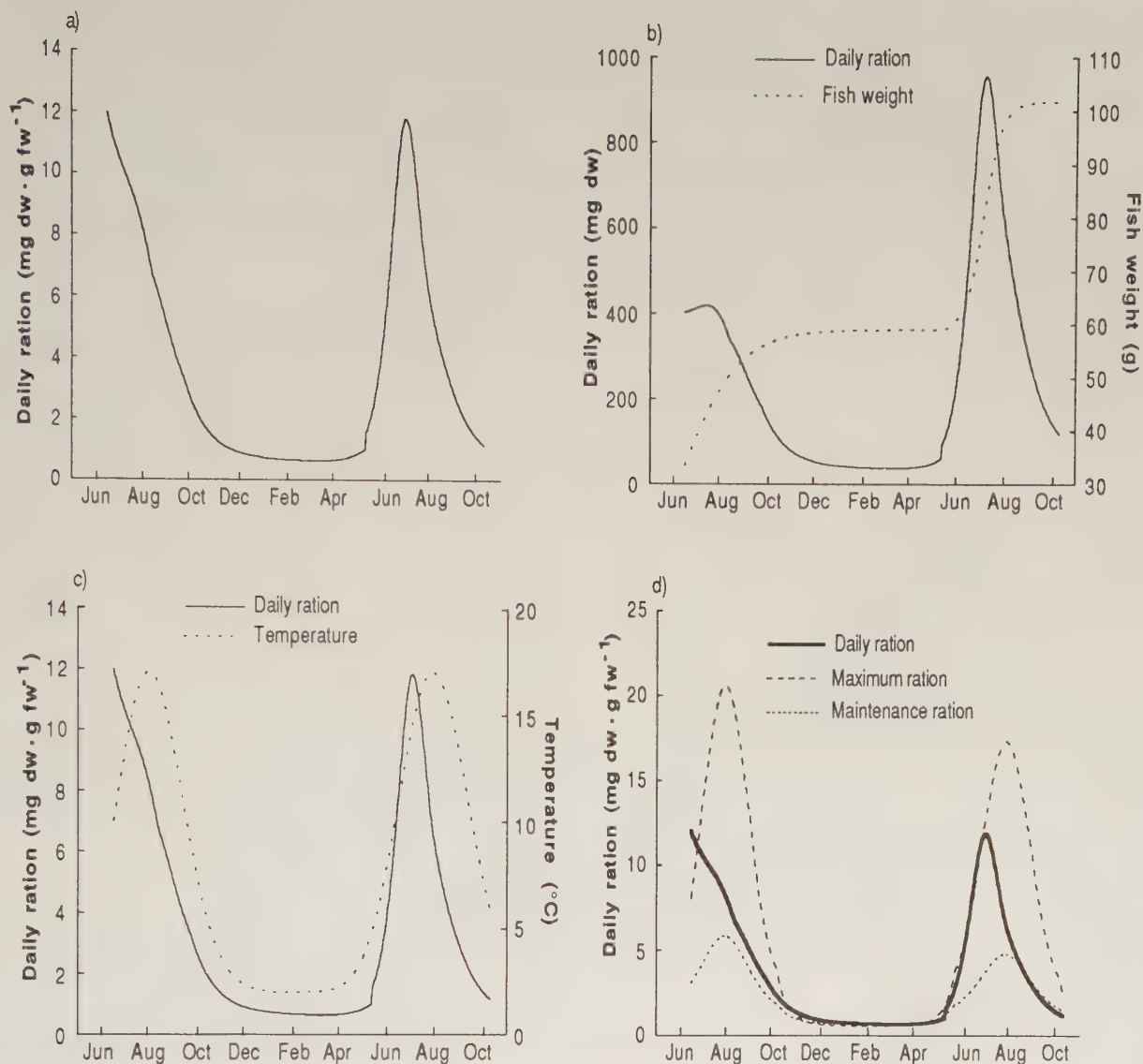


FIG. 3. Rations, from June 1988 to October 1989, for brown trout that hatched in spring 1986. (a) Relative (weight-specific) daily ration, (b) absolute daily ration and fish weight, (c) relative daily ration and ambient temperature, and (d) relative daily ration and estimated maximum and maintenance rations (Elliott 1975a, 1975b, 1975c).

TABLE 2. Relative (weight-specific) daily ration ($\text{mg dw} \cdot \text{g fw}^{-1}$, 95% C.L.) for brown trout estimated by the Eggers (1977) method.

Date	Year	Temperature (°C)	Fish weight (g)	Daily ration
11 June	1987	10.1	100	6.52 (6.19–6.85)
21 July	1987	17.4	80	14.12 (13.20–15.04)
2 Sept.	1987	10.6	101	2.05 (1.87–2.23)
27 Oct.	1987	5.0	70	1.43 (1.33–1.53)
Season	1987		860	
25 May	1989	7.8	86	7.22
27 July	1989	15.7	70	10.97
Season	1989		660	

performed at one temperature only. The absorption of energy from food by brown trout has been found to vary with temperature and ration size (Elliott 1976). The absorption of energy increases by approximately 15% from maximum ration at 3°C to small rations (10% of maximum) at 15°C. If the absorption of radiocesium varies in a similar fashion with changes in temperature and ration size, we would expect absorption efficien-

cies to vary less than 10% for brown trout from Lake Høysjøen because the rations are large at high and small at low temperatures. A 10% variability in absorption efficiency would result in only small changes in estimates of the daily ration. Some error may have been introduced into estimates by excluding the fast excretion rate from the computations. At equilibrium, however, the body compartment from which radiocesium is excreted quickly only represents a few percentage of the total body burden (Kolehmainen 1974), and the errors introduced by ignoring fast excretion are expected to be small.

As a general method for estimating food consumption by fish, the radioisotope method should be applicable for a large variety of fish species, prey types, and lakes. In contrast with other methods, such as the Elliott and Persson (1978) and Eggers (1977) methods, the radioisotope method is not restricted to fish that take small prey. In this study, we determined the absorption efficiency of ^{134}Cs from fish muscle, thus allowing estimates of daily ration for piscivorous brown trout. In order for the radioisotope method to be used in estimation of daily ration, information about both radiocesium absorption

TABLE 3. Relative daily ration (mean) and food consumption (mg dw·g fw⁻¹) for brown trout estimated by the Eggers (1977) and radioisotope methods (mean of all age groups).

Period	Year	Days	Eggers (1977) method		Radioisotope method	
			Daily ration	Food consumption	Daily ration	Food consumption
July–Sept.	1987		8.1		8.3	
Sept.–Oct.	1987		1.7		1.2	
July–Oct.	1987	98	4.5	441.0	4.3	422.9
June–Sept.	1988	100			7.3	728.1
May–July	1989	63	9.1	573.3	9.1	573.3

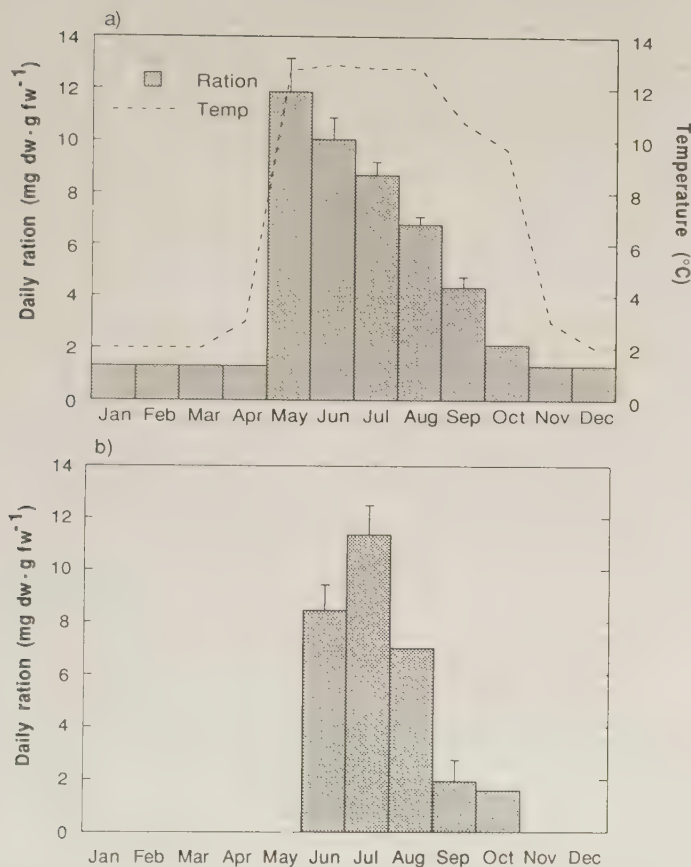


FIG. 4. Mean relative (weight-specific) daily ration (+SD) for brown trout at different months estimated by (a) the radioisotope method and (b) the Eggers (1977) method. Estimates from all observed years are pooled. The broken line represents water temperature during the same months.

and retention must be available. This requires laboratory studies to be conducted, but estimates of gastric evacuation rates determined in the laboratory are needed in order to apply the Elliott and Persson (1978) and Eggers (1977) methods to the estimation of food consumption of wild fish populations.

The radioisotope method is not restricted to radiocesium-contaminated lakes, since the method may be applied using other radioactive or stable isotopes, provided that the turnover of the isotopes is known. For example, in a lake in Colorado, USA, rainbow trout food consumption was estimated by adding stable cesium (¹³³Cs) to the lake (Hakonson et al. 1975), and the addition of stable cesium may be useful in smaller experimental water bodies. However, the use of gamma-emitting radioactive isotopes, such as ¹³⁷Cs from the Chernobyl fallout measured in the present study, has widest application because

such isotopes are easily measured. The method described in this paper is applicable to fish and prey radioactivity exceeding 100 Bq·kg wet weight⁻¹ and can be used in a number of systems.

The radioisotope method is best applied in lakes where the radioactivity levels of predator and prey have reached equilibrium. The method can probably also be used for uncontaminated organisms released into contaminated lakes, but under such circumstances, errors introduced due to disregarding the fast excretion component will be larger.

Acknowledgments

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La périodicité de la croissance chez la femelle de l'esturgeon jaune (*Acipenser fulvescens*) du fleuve Saint-Laurent est-elle reliée à la périodicité de la reproduction?

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La mesure de la distance interannuli sur des coupes transversales du premier rayon de la nageoire pectorale de 125 esturgeons jaunes (*Acipenser fulvescens*) femelles du fleuve Saint-Laurent âgées de 24 ans et plus a permis de tester la correspondance entre les profils d'accroissements en marge du rayon et le stade de maturité du poisson. Pour chacun des 21 spécimens de 34 ans et plus, ainsi que pour les spécimens de Roussow (1957, J. Fish. Res. Board Can. 14: 553–572), provenant de l'Outaouais supérieur, les accroissements interannuli, considérés comme une série temporelle, ont été analysés par le périodogramme de contingence. À l'instar de Roussow, l'âge moyen de la première fraye a été déterminé en utilisant l'âge à la fin du premier resserrement d'annuli. Seulement 3 des 21 femelles de 34 ans et plus montraient une alternance typique de bandes serrées et larges. Les cycles les plus fréquents révélés par le périodogramme sont de 5 à 11 ans, comparativement à 6 à 9 ans chez les spécimens de Roussow. Nous n'avons pas trouvé de correspondance significative entre le profil des cinq derniers accroissements interannuli et l'état de maturité du poisson. L'âge moyen de la première fraye estimé (19 ans) est inférieur à l'âge moyen de la maturité sexuelle obtenu par l'examen des gonades (26 ans).

Measurements of annual increments on cross-sections of the first ray of the pectoral fin of 125 St. Lawrence River female lake sturgeon (*Acipenser fulvescens*) aged 24 yr and older were used to test the correspondance between growth patterns at the margin of the sections and the state of maturity of the fish. For each of the 21 females aged 34 yr and older, and for the upper Ottawa River specimens presented by Roussow (1957, J. Fish. Res. Board Can. 14: 553–572), annual increments were treated as a temporal series and analysed with the contingency periodogram. The mean age at first spawning was determined using the age at the end of the first belt of crowded annuli, following Roussow. Only 3 of the 21 females aged 34 yr and older showed a typical succession of belts of large and narrow annuli. The most frequent periods were 5–11 yr, using the periodogram, as compared with 6–9 yr for Roussow's specimens. No significant correspondance was found between the pattern of the last five annual increments and the state of maturity. The mean age at first spawning, estimated at 19 yr by this technique, is lower than the mean age of sexual maturity determined for St. Lawrence River females based on the examination of the gonads (26 yr).

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Roussow (1957) a montré que l'on pouvait utiliser les coupes pratiquées dans le rayon marginal de la nageoire pectorale de l'esturgeon jaune (*Acipenser fulvescens*) pour déterminer l'âge, mais aussi l'âge à la première fraye, le sexe (la fréquence de maturation étant différente entre mâles et femelles) et les intervalles entre les frayes. En ce qui a trait à l'intervalle entre les périodes de reproduction, Roussow (1957) a associé, de façon qualitative, la présence de bandes d'annuli très rapprochés (« belts of crowded annuli », en marge du rayon, à la période précédant immédiatement la fraye. Le premier annulus large faisant suite à ces bandes d'annuli rapprochés serait déposé l'année même de la fraye, ou l'année suivante. En analysant les données sur la croissance et l'état de maturité des gonades de 24 spécimens (17 femelles et 7 mâles) capturés pendant la période de reproduction, Roussow (1957) a montré que l'intervalle entre les frayes consécutives variait entre 7 et 9.5 ans chez les femelles; il était de 7 ans chez les mâles.

Depuis la publication du travail de Roussow (1957), d'autres auteurs ont mentionné la présence de ces bandes d'annuli rapprochés sur les coupes de rayon marginal de la nageoire pectorale de l'esturgeon jaune (v.g. Wilson 1987), mais aucun n'a tenté de vérifier de façon plus approfondie l'existence d'une relation significative entre la périodicité de la croissance et la périodicité de la reproduction chez cette espèce. Le problème de l'évaluation de la périodicité de la reproduction prend une importance cruciale pour la gestion des pêches, particulièrement dans le cas d'une espèce longévive et aux frayes espacées dans le temps, comme l'esturgeon. L'objectif du présent travail consiste donc à vérifier, pour les esturgeons jaunes des lacs Saint-Louis et Saint-Pierre, l'hypothèse de Roussow (1957) à l'effet qu'il existe une périodicité de croissance et que le profil de dépôt des derniers annuli sur le rayon marginal de la nageoire pectorale est en relation directe avec le stade de maturité du spécimen. Si tel était le cas, l'estimation de la période moyenne

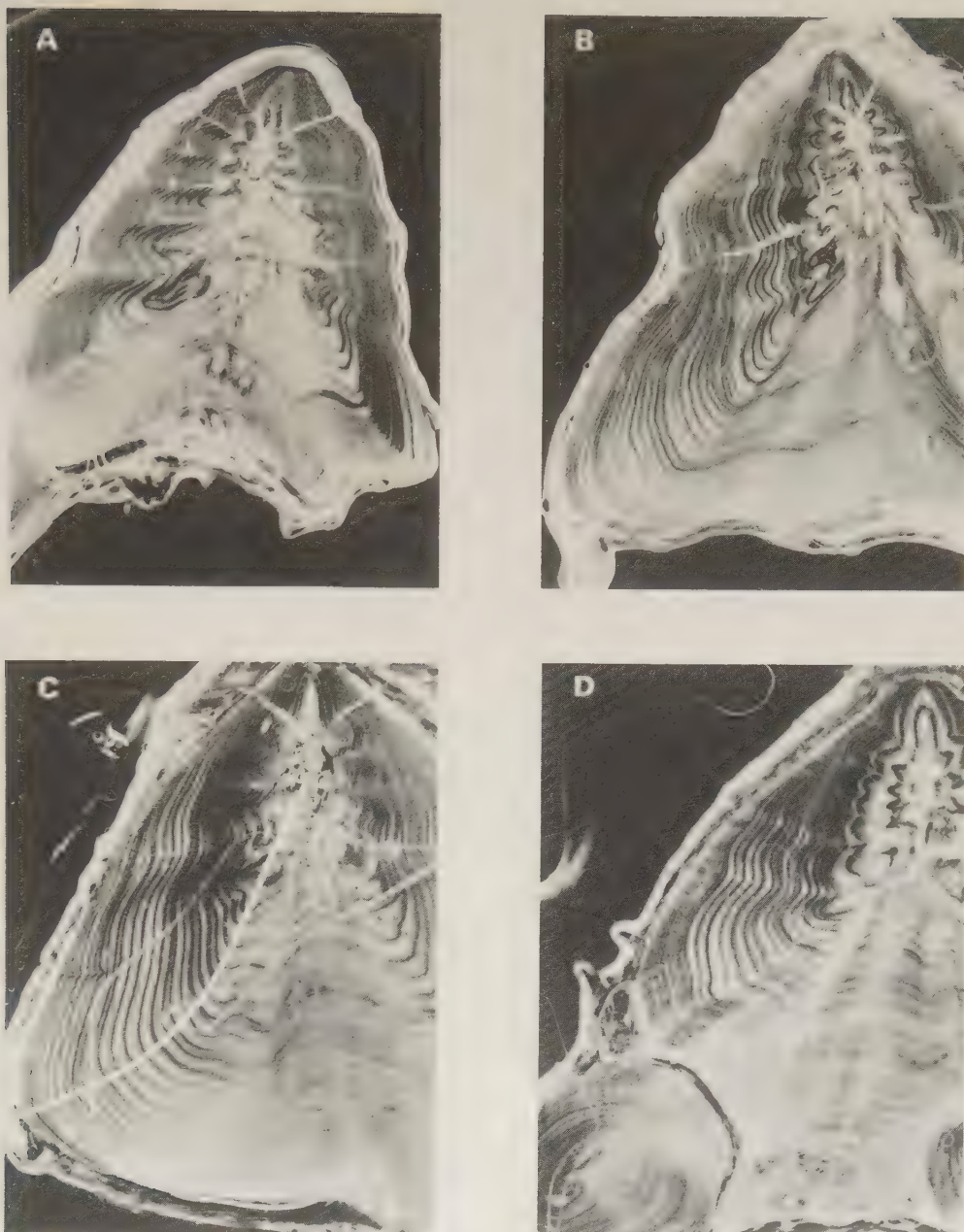


FIG. 1. Exemples de classification des profils de croissance à la marge du rayon de la nageoire pectorale. (A) Large : deux accroissements large à la marge. (B) Serré : trois accroissements serrés précédés d'accroissements larges. (C) Régulier : diminution graduelle des accroissements à mesure qu'on s'approche de la marge; la courbe blanche désigne l'axe de mesure des accroissements interannuli. (D) Régulier : plus de 10 accroissements serrés à la marge, précédés d'accroissements larges.

observée à partir des accroissements interannuli constituerait une approximation de la période moyenne séparant deux frayes.

Matériel et méthodes

Mesures, prélèvements et observations sur les spécimens

Notre étude a porté uniquement sur les esturgeons femelles. Cette décision repose sur le fait que pour révéler l'existence d'une périodicité de croissance reliée éventuellement à la reproduction, on doit utiliser des spécimens très âgés, de façon à ce que l'algorithme de calcul puisse extraire les périodes avec fiabilité. Or dans le cas de la pêche commerciale du fleuve Saint-Laurent, la majorité des spécimens dépassant 30 ans sont des femelles. Les spécimens proviennent d'un échantillon de

1 782 esturgeons capturés entre 1982 et 1986 par les pêcheurs commerciaux de deux élargissements du fleuve Saint-Laurent soit les lacs Saint-Louis et Saint-Pierre situés respectivement en amont et en aval de Montréal. De ce nombre, nous avons utilisé 118 à 125 femelles qui étaient âgées de 24 ans et plus; le détail des effectifs en fonction des analyses sera exposé plus loin.

Au lac Saint-Louis, les mesures (longueur totale, circonférence maximale et poids) et prélèvements (segment de gonade et premier rayon des nageoires pectorales) ont été effectués par le personnel du Ministère du Loisir, de la Chasse et de la Pêche du Québec (MLCP), chez les pêcheurs commerciaux, au moment de l'éviscération des prises. Les segments de gonade ont été fixés au formol 5 %. Au lac Saint-

TABLEAU 1. Description des stades de maturité des gonades femelles (tiré de Goyette *et al.* 1987).

Stade	Gonade	Ovocyte
1,0	Apparence « pointillée » à l'oeil nu ^a ; feuillet ovaires détachés	Diamètre : 0,3 mm
1,5	Petits oeufs bien visibles à l'oeil nu	Diamètre : 0,3 à 0,8 mm
1,9	Stade de réorganisation : feuillet très détachés mais fermes; présence d'oeufs en résorption encore entiers ou qui se détachent en petits granules noirs	Deux tailles : 0,3 et 0,7 à 1,2 mm
2,0	Ovocytes facilement distinguables à l'oeil nu, de couleur jaune pâle	Diamètre : 0,9 à 1,4 mm; présence de petits ovocytes blancs
3,0		Diamètre : 1,4 à 2,0 mm; présence de petits ovocytes blancs
4,0		Diamètre : 2,2 à 2,5 mm; présence de petits ovocytes blancs
5,0	Oeufs bruns avec un pôle cerclé de couronnes noirâtres	Diamètre 2,5 à 3,5 mm; présence de petits ovocytes blancs
6,0	Stade post-fraye : reste quelques oeufs noirs non-relâchés; feuillet blanchâtres, flasques	Diamètre des ovocytes blancs : 0,4 à 0,9 mm

^aSur les gonades conservées dans le formol, un dépôt graisseux empêche parfois de voir cet aspect pointillé. On doit alors gratter la surface afin de la dégager de ce dépôt.

Pierre, les mesures et prélèvements furent effectués par les pêcheurs commerciaux moyennant une prime de 5,00 \$ pour chaque poisson retenu. Les gonades ont été conservées au congélateur, puis décongelées et fixées au formol 5 %.

Les coupes du rayon marginal de la nageoire pectorale ont été effectuées au moyen de deux scies électriques rotatives, la première de marque Bronwill (modèle 77), donnant une précision de coupe de $\pm 25 \mu\text{m}$, et la seconde de marque Isomet (modèle 11-180), donnant une précision de coupe de $\pm 10 \mu\text{m}$. En fonction de l'opacité d'une première coupe d'essai mesurant $275 \mu\text{m}$ d'épaisseur, l'épaisseur des coupes utilisées pour les lectures pouvait varier entre 150 et $350 \mu\text{m}$. Les coupes ont été fixées sur lame de microscope au moyen d'un mélange à volume égal de toluène et de diatex. L'utilisation d'un lecteur de microfiches (Bell and Howell, modèle Spacemaster, série 1289A) a permis l'observation des coupes et leur photocopie au grossissement choisi (24 ou $48\times$). Les photocopies des coupes ont été examinées qualitativement afin de déterminer le profil de croissance des cinq derniers annuli, l'âge de la première fraye et la présence de cycles d'alternance de bandes d'annuli serrés et larges, à la manière de Roussow. Les mesures des accroissements interannuli ont été effectuées directement sur les photocopies. Une ligne fut tracée au moyen d'une courbe française, à partir du point situé à mi-distance entre les extrémités des deuxièmes branches du premier annulus (sapin de Roussow 1957), en suivant l'axe de croissance maximum (fig. 1C). Les distances interannuli sur la courbe ont été saisies au moyen d'une table digitalisante (Houston Instruments, modèle DT11) et du logiciel de rétrocalcul DISBCAL (S. Middlemis. 1983. Voyageur Fisheries Consulting, RT 1, Box 128A, Somerset, WI 54025, USA) que nous avons modifié pour nos besoins. Le tout était relié à un micro-ordinateur de marque Sperry PC. Le lecteur intéressé pourra trouver dans Goyette *et al.* (1987) plus de détails concernant la méthodologie de réalisation et d'interprétation des coupes.

L'état de maturité des poissons fut déterminé par examen macroscopique des gonades, par l'examen de coupes histologiques pour certains spécimens, et par la mesure des ovocytes au moyen d'un vernier, dans le cas des plus gros, et au moyen d'un oculaire micrométrique monté sur une loupe binoculaire, dans le cas des plus petits. Pour la description de l'état de maturité des gonades, nous avons précisé certaines étapes de la clé de Cuvier (1966), en ajoutant une décimale au numéro du stade dont elles se rapprochent le plus dans l'ordre chronologique de la maturation (tableau 1). Les esturgeons immatures se situent aux stades 1,0 et 1,5. Les stades 2,0, 3,0 et 4,0 constituent des étapes de maturation des ovocytes; au stade 5,0, les ovocytes ont atteint la taille à laquelle ils seront pondus. Au stade 6,0, les femelles ont frayé dans l'année courante et leurs gonades sont caractéristiques : flasques, blanchâtres et portant encore des oeufs bruns qui n'ont pas été relâchés et dont la résorption n'est pas amorcée. Une étape supplémentaire de récupération a été ajoutée, soit le stade 1,9. À ce stade, les poissons auraient déjà frayé, mais pas durant l'année, car les gonades sont plus fermes et les oeufs qui n'ont pas été évacués sont en résorption avancée. Cette étape a été placée tout juste avant le stade 2,0 en raison du diamètre des plus gros ovocytes qui varie de 0,7 à 1,2 mm au stade 1,9 et de 0,9 à 1,4 mm au stade 2,0. Le processus de maturation reprend ensuite au stade 2,0 sans repasser par les stades 1,0 et 1,5.

Traitement statistique

Périodicité

Tel que mentionné plus haut, seuls les spécimens les plus âgés ont été retenus pour l'étude de la périodicité de croissance. En effet, pour mettre en évidence une périodicité de croissance liée au cycle de la reproduction, on doit travailler sur les

portions des séries correspondant aux âges où le poisson est susceptible d'être affecté par le cycle de reproduction. Dans les cas les plus extrêmes (séries courtes), nous avons abaissé jusqu'à 14 ans l'âge de départ des séries destinées à l'étude de la périodicité, la plupart des âges de départ étant fixés à 19 ans. Comme l'analyse statistique des séries ne permet d'étudier que des périodes ou des longueurs d'ondes égales à la moitié de la longueur de la série, et comme les chiffres avancés dans la littérature situaient la périodicité de la reproduction des esturgeons femelles entre quatre et dix ans (Roussow 1957; Cuerrier 1966; Magnin 1966), nous avons jugé qu'idéalement les séries étudiées devaient avoir une vingtaine d'observations ou plus. Conséquemment, seules les 21 femelles de 34 ans et plus dont nous disposions ont été retenues aux fins de l'analyse des séries.

Dans le but de valider, ou à tout le moins de tester le mode d'analyse choisi, nous avons également effectué une analyse témoin sur des séries de mesures d'accroissements interannuli obtenues à partir d'agrandissements de reproductions de coupes de rayons marginaux d'esturgeon présentées par Roussow (1957). Selon cet auteur, ces reproductions correspondaient à des cas typiques de périodicité de croissance reliée à la maturation sexuelle. Nous avons choisi de fixer à 15 ans l'âge de départ des séries et de conserver les sujets de 30 ans et plus. Les mesures d'accroissements ont été obtenues et traitées de la même façon que sur les coupes effectuées par notre équipe.

La technique choisie pour l'analyse des séries est basée sur le périodogramme de contingence tel que décrit par Legendre *et al.* (1981). Cet outil statistique présente l'intérêt de permettre le travail à partir de séries relativement courtes (P. Legendre, Département de Biologie, Université de Montréal, C.P. 6204, Succ. A, Montréal (Québec) H3C 3T4, Canada, comm. pers.). Le programme Period du logiciel R a été utilisé dans les calculs. Préalablement à l'utilisation du périodogramme, nous avons, conformément aux recommandations de Legendre et Legendre (1984), vérifié si chacune des séries à l'étude présentait une tendance afin de l'extraire le cas échéant. L'identification des séries présentant une tendance monotone significative a été effectuée de façon formelle à l'aide de tests de rang de Kendall menés sur chaque série. Pour l'extraction de la tendance, nous avons utilisé la méthode des différences successives où chaque valeur est remplacée par sa différence avec la valeur suivante (procédure Box-Jenkins dans le progiciel SPSS^x).

L'interprétation des périodogrammes de contingence doit être adaptée à chaque cas. En effet, cet algorithme, qui peut mettre en évidence plus d'une période par série, a tendance à faire ressortir aussi les harmoniques associées aux périodes significatives. De plus, l'identification des harmoniques peut se compliquer lorsqu'elles se présentent comme des harmoniques imparfaites (ex. : $8 = (15, 16, 17)$). Pour procéder au filtrage des périodes identifiées par le périodogramme de contingence, nous avons appliqué différentes recommandations faites par un des auteurs de la méthode (P. Legendre, comm. pers.). Dans un premier temps, nous avons vérifié la constance des périodes identifiées en reprenant les essais basés sur les valeurs brutes pour les effectuer à partir des valeurs transformées en rangs. Deuxièmement, nous avons répété tous les essais précédemment menés en imposant au périodogramme de séparer les valeurs de départ de chaque série en quatre classes, l'algorithme interne du programme ayant choisi pour la très grande majorité des séries étudiées un nombre de classes égal à deux ou trois. Troisièmement, nous avons accordé un poids supérieur aux périodes ayant un niveau de confiance statistique supérieur. Enfin, il nous est apparu peu

probable que des périodicités de plus de 20 ans aient un rapport étroit avec le cycle de reproduction à moins qu'elles ne soient des harmoniques de périodes plus courtes. Nous avons donc considéré comme vraiment significatives les périodes qui revenaient dans plus de la moitié des essais effectués (3/4) ou étaient identifiées dans la moitié des essais effectués avec un niveau de confiance statistique supérieur au seuil choisi au départ ($P \leq 0,05$), et qui avaient une longueur égale ou inférieure à 20.

Relation entre le profil de croissance et le stade de maturité

Si on accepte la théorie des ceintures d'annuli rapprochés de Roussow (1957), on doit admettre qu'il existe une relation entre le profil des derniers accroissements interannuli en marge des coupes et l'état de maturité sexuelle du poisson à la capture. Conséquemment, si le cycle de reproduction des esturgeons femelles a une durée de quelques années, le profil des derniers accroissements interannuli devrait différer entre une femelle qui se prépare à frayer, une femelle en récupération suite à la fraye et une femelle immature.

Nous avons utilisé deux approches pour mettre en évidence une éventuelle relation entre le profil des derniers accroissements interannuli et l'état de maturité sexuelle à la capture. En premier lieu, les cinq derniers annuli des femelles de 24 ans et plus ont été classifiés qualitativement en catégories inspirées des observations de Roussow (1957). Ce dernier émettait l'hypothèse que la reprise de la croissance avait lieu la même année, ou plus probablement l'année suivant la fraye; les femelles en voie de frayer devaient donc montrer une croissance plus faible (bande serrée) tandis qu'une femelle en récupération après la fraye montrerait un ou deux annuli distancés. La première classification comportait six catégories de profil de croissance en fonction du nombre d'annuli serrés ou larges à partir de la marge. Par la suite, afin de ne pas présumer de la longueur des cycles, nous avons regroupé les profils en trois classes (fig. 1), soit : *large* (au moins un accroissement large à la marge, précédé d'accroissements serrés), *serré* (au moins un accroissement serré à la marge, précédé d'accroissements larges) et *régulier* (plus de 10 années d'une croissance stable). Puisque la croissance diminue avec l'âge, on distingue les annuli qui se resserrent brusquement (serrés) des annuli qui se resserrent graduellement à la marge du rayon (réguliers). Notons que les resserrements et élargissements notés ici étaient rarement aussi prononcés que ceux des spécimens de Roussow et que seul un examen attentif tenant compte de la croissance générale permettait un classement ($N = 118$; des 125 spécimens disponibles, 7 ont été rejetés parce que leur classement était impossible). Ensuite, les stades de maturité ont été regroupés selon trois états plus généraux de maturité sexuelle, soit femelle immature (stades 1,0 et 1,5), femelle mature (stades 2,0, 3,0, 4,0 et 5,0) et femelle en récupération (stades 6,0 et 1,9).

En deuxième lieu, les variations de croissance des cinq derniers annuli ont été analysées quantitativement par classification automatique. Pour cette analyse les femelles retenues sont les esturgeons de 24 ans et plus, au nombre de 125 (22 provenant du lac Saint-Louis, 103 du lac Saint-Pierre). La classification automatique a été effectuée avec un algorithme de groupement à lien intermédiaire avec probabilité de regroupement à 50 %, à partir d'une matrice de corrélation (r de Pearson). Les variables de départ étaient pour chaque poisson les cinq derniers accroissements interannuli. La matrice de corrélation et le groupement hiérarchique ont respectivement été obtenus à l'aide des procédures SIMIL et INTERLINK du logiciel R, sur l'ordinateur AMDAHL de l'Université du Québec à Montréal.

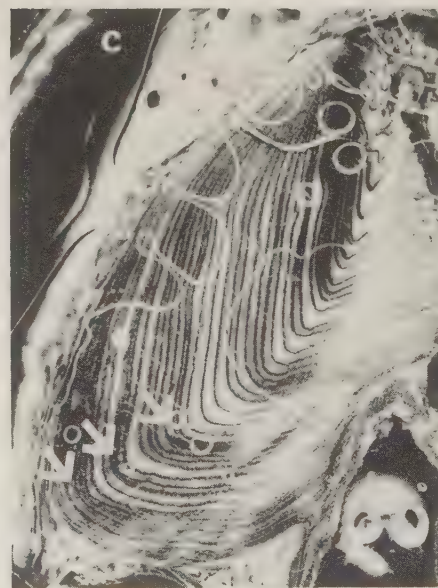
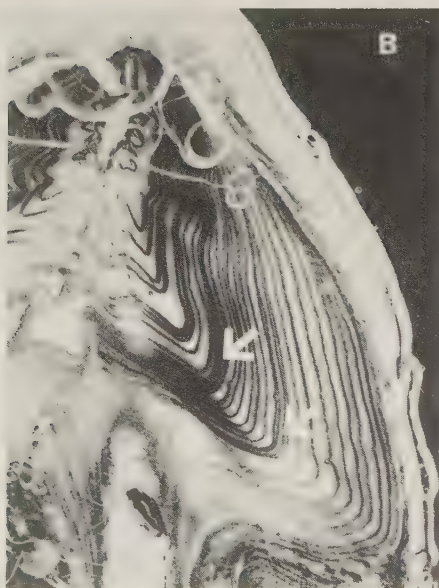
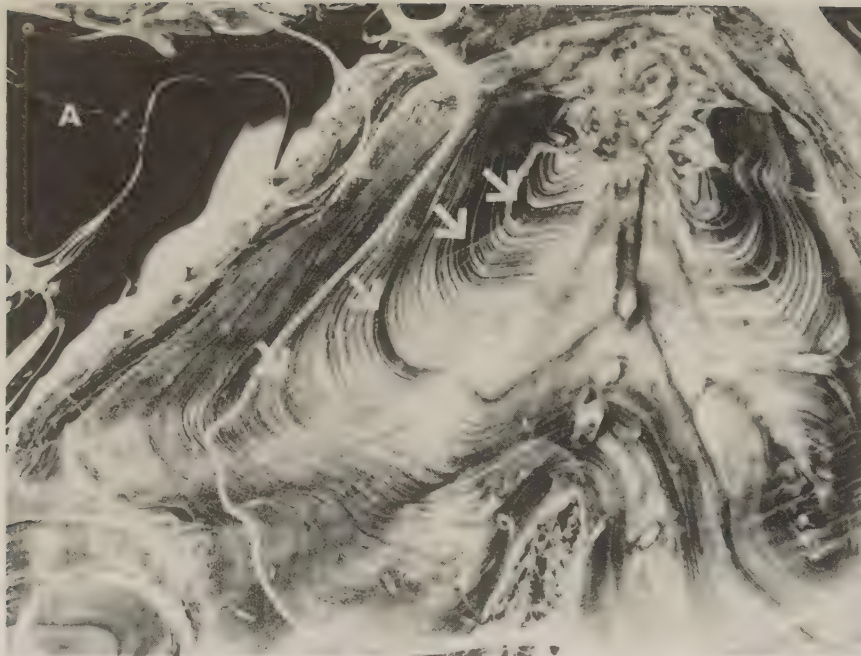


FIG. 2. Illustrations de femelles qui présentent des cycles de croissance. Les resserrements sont désignés par des flèches. (A) 96 ans; quatre resserrements présents, les annuli suivants sont uniformément serrés. (B), 35 ans; deux resserrements présents, les annuli suivants sont uniformément larges. (C) 43 ans; trois resserrements présents.

Âge moyen à la première fraye

À l'instar de Roussow (1957), nous avons également tenté de déterminer l'âge moyen à la première fraye en utilisant l'âge à la fin du premier resserrement impliquant au moins trois annuli. Les resserrements finissant avant l'âge de 13 ans ont été écartés puisque l'âge de la maturité sexuelle (âge où les gonades de 50 % des femelles ont atteint ou dépassé le stade 2,0) est généralement estimé à un minimum de 23 ans dans les différents plans d'eau de l'Amérique du Nord (Harkness et Dymond 1961), que la plus jeune femelle de stade 5 trouvée dans les captures commerciales du fleuve Saint-Laurent avait

16 ans et qu'enfin 97 % des femelles de 16 à 19 ans de notre échantillon ($N = 94$) n'avaient pas atteint le stade 2.

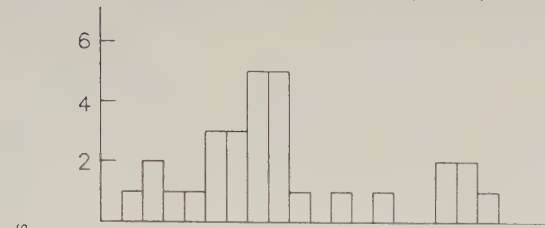
Résultats

Périodicité de croissance

L'examen visuel des coupes du rayon des femelles de 34 ans et plus ne permet pas de reconnaître une alternance de bandes d'annuli serrés puis larges aussi typiques que celles présentées par Roussow; seulement 3 spécimens sur 21 présentent de telles alternances et de façon irrégulière (fig. 2).

REPRODUCTIONS TIRÉES DE ROUSSOW

29 périodes constantes / 12 poissons



ESTURGEONS FEMELLES DE 35 ANS ET PLUS LAC SAINT-LOUIS ET LAC SAINT-PIERRE

35 périodes constantes / 21 poissons

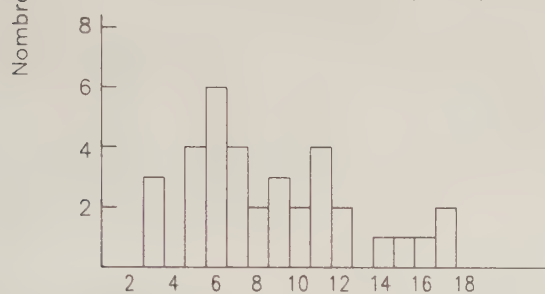


FIG. 3. Fréquence d'apparition des périodes les plus constantes pour l'ensemble des périodogrammes effectués.

TABLEAU 2. Répartition des profils de croissance des cinq derniers annuli classifiés qualitativement en fonction des stades de maturité pour les femelles de 24 ans et plus.

Profil de croissance	Stades de maturité			Total
	Immature	Mature	En récupération	
Large	3	3	5	11
Serré	7	6	8	21
Régulier	17	42	27	86
Total	27	51	40	118

La fig. 3 présente une synthèse des résultats obtenus suite à l'épuration visant à ne conserver que les périodes les plus constantes. Bien que le nombre de ces périodes soit trop faible pour permettre des vérifications statistiques rigoureuses, l'observation de ces résultats permet de dégager les éléments suivants. Premièrement, en accord avec les observations de Roussow (1957), les résultats des périodogrammes appliqués aux reproductions présentées par cet auteur révèlent que le mode des fréquences d'apparition des périodes significatives se situe autour de 8-9 ans. Deuxièmement, pour les esturgeons des lacs Saint-Louis et Saint-Pierre, l'étalement des fréquences d'apparition des périodes significatives est plus grand, avec un mode principal se situant à 6 ans et des modes secondaires à 11 et 9 ans. Troisièmement, les exemples présentés par Roussow (1957) permettent de dégager un nombre moyen de périodes par poisson supérieur à ce que nous observons pour les spécimens du fleuve Saint-Laurent (2,4 vs. 1,7).

Relation entre les accroissements interannuli marginaux et l'état de maturité

La classification qualitative des accroissements interannuli ne semble pas correspondre avec l'état de maturité sexuelle

TABLEAU 3. Composition des groupes résultant de la classification automatique selon les stades regroupés de maturité sexuelle.

Groupe ^a	Stades regroupés de maturité sexuelle			Total
	Immature	Matures	En récupération	
1 ^b	8	21	14	43
2 ^b	5	9	4	18
3 ^b	8	8	9	25
4 ^b	3	12	9	24
5	4	1	4	9
6	2	3	1	6
Total	30	54	41	125

^aNiveau de regroupement fixé à 0,3.

^bGroupes conservés pour le test du khi carré sur la distribution des états de maturité sexuelle.

(tableau 2) aussi étroitement que le constatait Roussow (1957). En effet, aucun profil d'accroissement ne correspond à un stade de maturité particulier. On remarque que les accroissements réguliers constituent le profil le plus répandu, et ce dans toutes les classes de maturité. Les femelles en récupération, qui devraient présenter au moins un accroissement plus large à la marge du rayon montrent, dans notre échantillon, une variété de profils d'accroissements interannuli. Les femelles matures (stades 2,0 à 5,0) devraient afficher une croissance plus lente à la marge; cependant, la majorité d'entre elles (82 %) présentent une croissance régulière, et 12 % montrent au moins deux annuli serrés à la marge. Les femelles immatures présentent principalement un profil de croissance régulier (63 %). En outre, 48 % ($N = 27$) des femelles immatures, qui ne devraient pas montrer de resserrement puisqu'elles n'ont jamais frayé, présentaient au moins une série d'annuli serrés sur l'ensemble de leurs années de croissance.

L'étude des groupements hiérarchiques en fonction des stades de maturité sexuelle n'amène pas de conclusions précises. Ainsi, l'analyse des groupes formés en fonction des stades regroupés (tableau 3) permet de vérifier la signification des quatre groupes contenant le plus d'objets. Les deux autres groupes ont dû être écartés du test de khi carré en raison de leurs effectifs trop faibles. Le résultat de ce test ne permet toutefois pas d'établir un rapport significatif entre les groupes formés en fonction du profil de leurs cinq accroissements interannuli marginaux et la maturité sexuelle des poissons ($P = 0.57$).

Devant ces résultats, nous avons tenté d'apporter des variantes à notre approche, comme par exemple de regrouper les esturgeons femelles qui venaient tout juste de frayer (stade 6,0) avec les esturgeons en maturation, plutôt qu'avec les esturgeons en récupération. Puis, nous avons effectué des analyses discriminantes sur les accroissements des cinq derniers annuli en fonction des stades de maturité. Les résultats n'ont pas été plus révélateurs. Ces analyses n'ont pas eu plus de succès pour trouver une correspondance significative entre le stade de maturité et les accroissements interannuli.

Âge moyen à la première fraye

Seulement 27 femelles sur 118 présentaient au moins un resserrement; l'âge moyen à la première fraye calculé pour ces femelles serait de 19 ans. Bien que cet estimé soit plus élevé que celui obtenu par Roussow au moyen de la même méthode (18 ans), il semble qu'il soit encore sous-estimé par rapport à l'âge moyen de la maturité sexuelle (26 ans) obtenu par l'observation des gonades (Goyette *et al.* 1987). Précisons que l'âge de la maturité sexuelle ne correspond pas à l'âge de la première

fraye puisqu'il existe un délai d'au moins quatre ans entre le moment où la gonade atteint le stade 2 (maturité sexuelle) et le moment de la fraye (stade 5).

Discussion

Nous insistons tout d'abord sur les difficultés rencontrées dans l'interprétation de la marge des coupes de rayons de nageoire de l'esturgeon jaune. Malgré le fait que l'épaisseur des coupes ait été ajustée en fonction du degré d'opacité d'une première coupe d'essai, le dénombrement et la mesure des annuli dans les secteurs où ces derniers sont très regroupés, formant les ceintures décrites par Roussow (1957), demeure toujours difficile. Nos observations à ce sujet rejoignent celles de Wilson (1987) à l'effet que la première bande d'annuli étroits est généralement facile à interpréter, mais qu'avec l'âge du poisson, les annuli inclus dans ces bandes, qui souvent ressemblent à un seul annulus particulièrement large, deviennent de plus en plus difficiles à dénombrer. Ceci est particulièrement vrai lorsque la bande est située en bordure de la coupe, qui présente souvent alors une apparence hyaline chez les poissons âgés.

Plusieurs auteurs souscrivent à la théorie de la correspondance croissance-stades de maturité sans pour autant que les fondements en aient été établis hors de tout doute. Par exemple, Dadswell (1979, *Acipenser brevirostrum*), Taubert (1980, *Acipenser brevirostrum*), Smith (1985, *Acipenser oxyrinchus*), Classen (1944, *Acipenser sturio*), Semakula and Larkin (1968, *Acipenser transmontanus*) et Xin *et al.* (1991, *Acipenser sinensis*) admettent de façon implicite ou explicite cette théorie. À l'opposé, on retrouve également des auteurs qui ont émis des doutes quant à la relation entre les ralentissements de croissance et le cycle de maturation des gonades de l'esturgeon : Shilov *et al.* (1971), Sunde (1961) et Wilson (1987). Roussow admet lui-même que des facteurs autres que la reproduction (conditions environnementales, état général de santé du poisson, accidents) peuvent influencer le rythme de croissance chez l'esturgeon. Pour notre part, nous n'avons observé que rarement des cas de périodicité de croissance aussi clairs que ceux présentés sous forme de croquis par Roussow. La caractéristique qui nous est apparue dominante sur les coupes de la première épine des nageoires pectorales est le resserrement accentué des anneaux de croissance avec l'âge. Cette observation est appuyée par le fait que, lors de l'étude des séries de mesures d'accroissement, nous avons décelé une tendance monotone chez 62 % (13/21) des esturgeons de notre échantillon, comparativement à seulement 25 % (3/12) pour les spécimens de Roussow (1957). Enfin, nous avons pu identifier en moyenne 1,7 période significative et constante par poisson chez les esturgeons âgés des lacs Saint-Louis et Saint-Pierre, comparativement à 2,4 pour les cas présentés par Roussow.

Il est possible que les résultats obtenus par Roussow (1957) sur les esturgeons de l'Outaouais supérieur ne soient pas applicables à d'autres milieux ou à tout le moins, pas aux populations du Saint-Laurent. Par exemple, les esturgeons des régions nordiques, en raison d'un budget énergétique moindre, pourraient présenter des signes plus évidents de périodicité de croissance. De plus, les périodes détectées par le périodogramme de contingence pourraient résulter de l'influence combinée des conditions environnementales, de l'état de santé du poisson et de la maturation des gonades.

Nous n'avons pas trouvé de correspondance entre le profil de croissance des cinq derniers annuli et le stade de maturité

sexuelle. S'il est impossible d'établir une telle relation qualitativement ou par des analyses statistiques plus fines, nous doutons que cette technique puisse être d'une grande utilité pour établir la fréquence de la reproduction ou l'âge moyen de la première fraye chez l'esturgeon jaune du fleuve Saint-Laurent, sans qu'elle soit entachée d'un biais considérable. D'autres approches devraient donc être privilégiées pour évaluer l'âge de la maturité sexuelle et la périodicité de la reproduction des esturgeons jaunes du Saint-Laurent.

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Effects of Sounds from a Geophysical Survey Device on Behavior of Captive Rockfish (*Sebastes* spp.)

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Behavior of rockfish (*Sebastes* spp.) exposed to air-gun sounds was examined to establish parameters in a subsequent fishing experiment to determine the effects of a geophysical survey device on fishing success. Rockfish observed in a field enclosure showed startle and alarm responses during 10-min exposures to sounds from a single 1639-cm³ air gun. For olive and black rockfish (*S. serranoides* and *S. melanops*), the threshold for the startle responses lay between 200 and 205 dB re 1 μ Pa. Under sound presentation, blue rockfish (*S. mystinus*) milled in increasingly tighter mills, and schools of black rockfish collapsed to the bottom. Vermilion (*S. miniatus*) and olive rockfish formed stationary schools near the bottom and, on sound presentation, either rose in the water column or moved to the bottom and became almost motionless. The general threshold for the alarm responses was about 180 dB re 1 μ Pa. Regression analyses of changes in depth distribution and shifts to active behaviors suggested that more subtle behavioral responses to sounds might become evident at 161 dB re 1 μ Pa. These initial responses were sustained only for a few minutes and may differ from those of unconfined fish.

Le comportement de sébastes (*Sebastes* spp.) exposés aux sons émis par un canon à air comprimé a été étudié afin d'établir les paramètres d'un essai de pêche visant à déterminer les effets des canons utilisés pour les levés géophysiques. Les sébastes observés dans une enceinte sur place ont présenté des réponses de surprise et d'alerte au cours d'expositions de 10 min aux sons émis par un canon à air comprimé de 1 639 cm³. Dans le cas des sébastes olive et noir (*S. serranoides* et *S. melanops*), le seuil de ces réponses se situait entre 200 et 205 dB à 1 μ Pa. Sous l'effet des ondes sonores, les sébastes bleus (*S. mystinus*) se sont mis à tourner en rond en groupes de plus en plus serrés tandis que les bancs de sébastes noirs se sont dirigés vers le fond. Les sébastes vermillon (*S. miniatus*) et olive formaient des bancs stationnaires à proximité du fond et, sous l'effet des ondes sonores, ils se sont élevés dans la colonne d'eau ou se sont déplacés vers le fond et y sont demeurés pratiquement sans bouger. Le seuil de la réponse d'alerte était généralement de 180 dB à 1 μ Pa. Des analyses par régression des modifications de la distribution selon la profondeur et de l'apparition de comportements actifs portent à croire à l'existence de réponses comportementales aux sons moins apparentes à partir de 161 dB à 1 μ Pa. Ces premières réponses n'étaient maintenues que pendant quelques minutes et pourraient différer de celles des poissons non confinés.

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There has been concern that sounds generated by air guns and other acoustic devices used in offshore oil and gas exploration have been affecting the commercial hook-and-line fishery for rockfish (*Sebastes* spp.) along the California coast. Experimental studies have indicated that sounds from nonexplosive survey devices such as air guns are not lethal to fish, and physiological effects have been reported for fish only within a few metres of air guns (Falk and Lawrence 1973; R. W. Weaver and R. J. Weinhold, Alaska Department of Fish and Game, unpubl. data). For fish, sounds from nonexplosive survey devices are much more likely to result in behavioral changes than physiological damage. Fish detect and respond to sounds (for a review, see Tavalga et al. 1981; Schwarz 1985), and loud, abrupt sounds may produce startle and alarm responses in fish (Blaxter et al. 1981; Blaxter and Hoss 1981; Schwarz

and Greer 1984). We are concerned here with the levels at which fish respond to sounds from geophysical survey devices and what their response is likely to be.

Air guns are the type of device most frequently used in geophysical surveys off California (Malme et al. 1986), and comparison of the known hearing abilities of fish with the characteristics of sounds from air guns indicates that marine fish can hear air-gun sounds. Malme et al. (1986) has found that single air guns and air-gun arrays produce sound in frequencies from 50 to 200 Hz and 20 to 150 Hz, respectively. Some air-gun arrays have frequency spectra extending to 500 Hz, and high-resolution seismic survey devices may have frequency spectra extending to 1000 Hz. Thus, the frequency spectra of the seismic survey devices cover the range of frequencies detected by most fish, for example, 50–3000 Hz for marine

fish in general (Platt and Popper 1981; Hawkins 1981) and 10–250 Hz specifically for Atlantic cod (*Gadus morhua*) (Buerkle 1968; Chapman and Hawkins 1973; Offutt 1974).

Available information indicates that marine fish are quite likely to detect air-gun sounds for some distance from their source. Given the close match between spectra, the distance over which fish are likely to hear survey sounds can be estimated from consideration of (1) the fish's detection threshold, (2) the effects of sound pulse duration and background noise, (3) the source level of the device, and (4) the transmission loss (Pearson et al. 1987). On the basis of field experiments with Atlantic cod (Chapman and Hawkins 1973), marine fish can be expected to exhibit a detection threshold for continuous sound of about 80 dB re 1 μ Pa (hereafter, dB will be expressed as relative to a reference level of 1 μ Pa). Because sound pulses of short duration can heighten the detection threshold (Hawkins 1981), perhaps by as much as 50 dB for air-gun sounds (Pearson et al. 1987), the detection threshold for air-gun sounds can be expected to be 130 dB. Malme et al. (1986) gave values of 222 and 250 dB at 1 m as typical source levels for single air guns and arrays of air guns, respectively, and Greene (1985) reported a source level equivalent to 255 dB at 1 m for a 28-gun array used off California. Given a 250-dB source level for an array and a 25 log(*R*) transmission loss as indicated by the data of Malme et al. (1986) and Greene (1985), a detection threshold estimated at 130 dB implies that a fish can hear survey sounds at a distance of 63 km. If the transmission loss is 35 log(*R*), typical of shallow water, the distance at which fish may hear sounds from arrays is estimated as 2.7 km.

Although available information indicates that fish may hear survey sounds at some distance, the levels at which rockfish would respond to such sounds or the nature of any responses have not been determined. Sound levels well above the detection threshold are needed to elicit behavioral responses in herring (Blaxter et al. 1981; Blaxter and Hoss 1981). Also, air guns produce sounds that have the abrupt onset or instantaneous rise time important in eliciting startle and alarm responses in herring (Blaxter et al. 1981; Schwarz and Greer 1984). Because experimental observations of behavioral responses of rockfish to air-gun sounds have not been made, our aim was to determine the thresholds at which air-gun sounds elicit behavioral responses in rockfish and to describe the nature of any such responses. Also, the results of these behavioral observations were to establish experimental parameters for a fishing experiment (Pearson et al. 1987; Skalski et al. 1992) subsequently conducted to determine the effects of air-gun sounds on fishing success.

Between July 13 and July 18, 1986, we conducted a field experiment to determine the threshold at which sounds from an air gun produced a startle response or other behavioral changes in captive rockfish. A field approach was used because the sound characteristics could not be simulated even in a large laboratory aquarium (Parvulescu 1967; Chapman and Hawkins 1973; Hawkins 1981; van den Berg and Schuijf 1985). In five trials, we presented air-gun sounds to rockfish held in a field enclosure and simultaneously observed their behavioral responses.

Materials and Methods

Study Area

The study area in Estero Bay, north of Morro Bay, California, was selected because it offered sheltered water of acceptable visibility close to locations where rockfish could be readily

captured (Fig. 1). During the experiment, seismic survey vessels were operating south of Pt. Sal, California, at least 65 km from our study area and, therefore, beyond the hearing of rockfish in our study area. After a survey to assess the visibility in the general area and ensure that the site was without potential sound shadows, the field enclosure was deployed off Cayucos, California, at approximately 35°25.8'N and 120°53.8'W. The enclosure location had a water depth of 14 m with a soft bottom of fine sand and silt. From the enclosure location, the bottom sloped southwards at approximately 10 m in 1 km.

Sound Production

A 35-m utility vessel, M/V *NAUTILUS*, supported the sound production systems. A single 1639-cm³ (100-in.³) air gun operated at 4500 psi (1 psi = 6.895 kPa) was chosen in order to provide a simple, well-defined sound source for the field trials. Also, an air gun was selected because this type of device is the most frequently used in geophysical surveys off California (Malme et al. 1986). The source level for this air gun was approximately 223 dB. A diesel-driven air compressor provided high-pressure air in sufficient volume to operate the gun at a firing rate of six pulses per minute, the rate used in all tests. The compressor was mounted on vibration isolation supports to reduce sound radiation into the water. The air gun was attached to an umbilical cable containing the air hoses and control wires and to a towing cable with a surface float. The float supported the gun at a depth of 6 m, a depth typical of industry practice. For close-range tests where precise control over the distance to source was needed, an inflatable boat was used to manually control the air-gun position.

Sound Monitoring

The sound monitoring, acoustic data acquisition, and data analysis systems were also installed on the M/V *NAUTILUS*. The source level and sound output of the air gun were monitored during all of the tests by a hydrophone 12 m away. A second hydrophone was installed on a spar buoy and deployed near or in the fish enclosure during the behavioral observations. This buoy was equipped with a radio transmitter to relay the acoustic signals back to the measurement and recording systems on the M/V *NAUTILUS*. For the first trial, in which the sound boat began discharging the air gun at 6 km from the enclosure, the buoy was anchored 21 m due north of the enclosure with the hydrophone at a depth of 3.7 m, which was equal to the depth of the floor of the enclosure. For the second and third trials, the buoy was deployed at the eastern side of the enclosure with the hydrophone at a depth of 2.4 m. The depth of the hydrophone was changed to position it at the midpoint of the depth distribution of the fish observed in the enclosure. For the remaining trials, the hydrophone was deployed in the center of the enclosure at a depth of 2.4 m.

The signals from the hydrophones were amplified and recorded using a multichannel analog tape recorder, a storage oscilloscope, and a strip chart recorder. A real-time narrow-band spectrum analyzer was used to analyze selected data samples during an experiment to obtain near-real-time hard copy records of pressure waveforms and pressure level spectra. All equipment was calibrated to obtain the system pressure sensitivity with a reference of 1 V/ μ Pa.

To estimate the potential effect of temperature and salinity gradients on sound velocity, we used a temperature and conductivity bridge to obtain depth profiles of sound speed to near

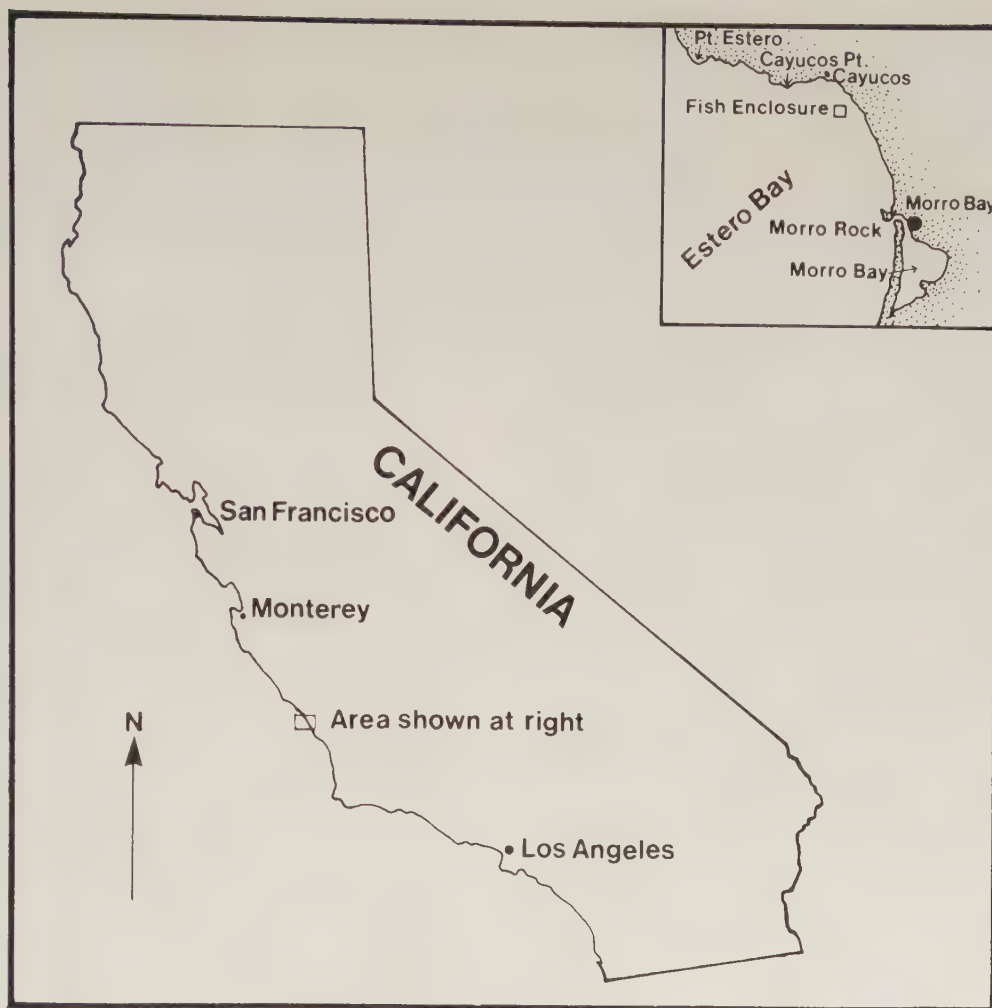


FIG. 1. Location of the fish enclosure near Cayucos Point used in the behavioral experiment.

bottom or 20 m. To measure the variation in the sound levels with depth, sound measurements were made within the enclosure with the air gun at a range of 50 m and with the hydrophone positioned at various depths within the center of the enclosure.

The signals received by the spar buoy hydrophone were recorded for all sound presentations and were analyzed on a pulse-by-pulse basis to determine sound exposure levels at the enclosure. We found that sampling of every third pulse was adequate to define the variability in exposure levels. The maximum positive and negative pressure values for each sampled signature were entered into a data file for each presentation. For the trials within metres of the enclosure, the acoustic travel time for the pulse was also measured to determine range. The effective peak pulse level in decibels re 1 μPa is defined as follows:

$$(1) \quad P_m = \frac{20 \log (P_+ - P_-)}{2} P_{\text{ref}}$$

where P_+ is the maximum positive pressure in micropascals, P_- is the maximum negative pressure (micropascals), and P_{ref} is the reference pressure, 1 μPa . The mean peak pressure level and standard deviation were determined for each sound presentation.

Experimental Enclosure

The field enclosure used for behavioral observation consisted of an octagonal PVC pipe frame and float system supporting a

net of 6 mm off-white knotless nylon mesh. The net was shaped as an octagonal prism with a flat top and flat bottom. The net measured 4.6 m across the diagonals and was 3.6 m deep. The enclosure was anchored at four points so that the net top was just below the water surface. A door in the center of the net top allowed observation of the captive fish with a viewing box from a rubber raft moored over the net top. For each trial, we adjusted the depth of the net floor so that all fish in the net were visible from the water surface through the viewing box.

Procedures for Trials

There were five behavioral trials with two to six sound presentations per trial. In Trials 1 and 2, the sound level during each succeeding 10-min presentation was increased by having the sound boat come to half the distance of the previous presentation. In subsequent trials, staircase regimes of sound levels were presented by directing the sound boat to decrease or increase the range depending on whether the fish showed any behavioral response. The staircase regime of sound levels was intended to estimate the threshold at which behavioral response occurred and is a standard approach to stimulus presentation for threshold determination (Cornsweet 1962). Behavior of the fish was observed before, during, and after sound exposure.

The afternoon before each day's trials, rockfish were captured near rock pinnacles in Estero Bay, California, by trolling with lures and barbless hooks in depths from 10 to 30 m. On

TABLE 1. Rockfish used in the behavioral experiment at Estero Bay, July 13–18, 1986.

Observed trial	Date of capture	Fish	Fish in enclosure
1	July 13	Blue rockfish, <i>S. mystinus</i>	13
		Olive rockfish, <i>S. serranoides</i>	7
2	July 14	Olive rockfish, <i>S. serranoides</i>	1
		Vermilion rockfish, <i>S. miniatus</i>	2
3	July 15	Olive rockfish, <i>S. serranoides</i>	6
		Vermilion rockfish, <i>S. miniatus</i>	7
4	July 15	Same fish as Trial 3	
5	July 16	Black rockfish, <i>S. melanops</i>	17
		Brown rockfish, <i>S. auriculatus</i>	1

capture, excess gas in the gas bladders of each fish was released by puncture with a hollow needle. Without release of excess gas, rockfish can be expected to suffer high mortality (Hart 1973). The fish were then placed into a holding tank with continuously flowing seawater on the F/V *BONNIE MARIETTA*. Within 3 h of capture, the rockfish were transferred into the field enclosure. Fish from the day's trials were released before introduction of new fish for the next day's trials. Fish were acclimated at least overnight before testing.

Each day's batch of fish varied in number and species composition because of variation in the daily catch (Table 1). An effort was made to test a variety of rockfish. For the first two trials, the selection strategy was to choose the most abundant fish in the catch to place 20 or all available fish into the enclosure. During the acclimation period for Trial 2, the large vermilion rockfish (*S. miniatus*) killed the smaller rockfish. Consequently, vermilion rockfish were not mixed with smaller rockfish thereafter. In Trial 5, three of 17 black rockfish (*S. melanops*) died during acclimation.

To determine thresholds for behavioral responses, five experimental trials (one per day) were conducted. Each trial began with a control observational period during which the fish were observed continuously through a viewing box for at least 30 min. All observations were made by one observer. Notes on the behavior of the fish were recorded by a second investigator on waterproof paper at 2-min intervals. Presentations of air-gun sounds were 10 min each and followed the control period. Behavioral observations were continuous, and notes on behavior were recorded at 1-min intervals. Two to six sound presentations were made per trial, depending on weather and the distance that the sound boat had to move between presentations. Between sound presentations, observations were made continuously for a minimum of 16 min with notes recorded at 2-min intervals. If more than 40 min separated the successive sound presentations because of the time needed to reposition the sound boat, observations for 10 min with notes recorded at 1- or 2-min intervals were made just after and just before the sound presentations. Observations were also made at 2-min intervals between these pre- and posttreatment observational periods. The sound levels measured during the presentations are given in the Results.

From the available information, we developed criteria for scoring each sound presentation. Before the experiment, three types of behavioral responses to loud, abrupt sounds were anticipated from observations of captive herring: avoidance, alarm, and startle (Blaxter et al. 1981; Schwarz and Greer 1984). Avoidance responses could not be observed in the field enclosure, although startle responses were. We also observed a combination of general increases in activity and changes in

schooling and water position, all of which we have categorized as "alarm" on the basis of analogy with the descriptions of Blaxter et al. (1981). For each sound presentation, the intensity of alarm and startle responses was scored according to the following criteria modified from Blaxter et al. (1981): 0, no response; 1/2, one or two fish respond; 1, several fish respond; 2, up to half the fish respond; 3, more than half the fish respond. Although these scores provided general indications of the behavioral responses, these data could not support the comparison of behavior during sound presentation with that before and after presentation.

Besides scoring intensity of alarm and startle responses, we used the 1- and 2-min observations to tabulate the number of fish observed in various categories of behavior as well as position in the water column. The behavioral categories were (1) holding position (undirected), (2) holding position (directed), (3) directed moving, (4) eddying, (5) milling, and (6) other moving. Similarly, the categories of water column position were (1) at the bottom, (2) in the lower one third, (3) in the middle one third, and (4) in the upper one third. In these tabulations, fish were recorded in both a behavioral category and a water column position. Descriptions of the behavioral categories appear in the Results.

Statistical Analyses

Graphical displays and multiple regression analyses were used to examine the relationship between sound exposure levels and changes in the vertical distribution and behavior of the fish in the field enclosures. These analyses were restricted to Trials 1, 3, 4, and 5 because Trial 2 (with three captive fish) had too few fish for appropriate tests of effects based on the percent change in activity patterns.

For the vertical distribution of the rockfish in the enclosure, a linear contrast of the form

$$(2) \quad L_i = (\text{percent of visible fish in upper two thirds of enclosure}) - (\text{percent of visible fish in lower one third of enclosure})$$

constructed for each individual observational period was plotted as a function of time and exposure. For response variable (2), the higher the value, the more fish were in the upper two thirds of the water column.

To reduce the dimensionality of the data in summary graphs, the behavior exhibited during a trial was translated to a linear contrast. For Trial 1 data, the 2-min observations were translated to the following linear contrast:

$$(3) \quad L_i = [3 (\text{number of fish milling}) \\ + 1 (\text{number of fish with directed swimming}) \\ - 1 (\text{number of fish eddying}) \\ - 3 (\text{number of fish holding})] \\ \div (\text{number of fish visible}).$$

The values of L_i in Equation 3 were then plotted as a function of time and treatment exposure. For Trials 3, 4, and 5, the individual observations on fish behavior were translated to the following linear contrast:

$$(4) \quad L_i = [3 (\text{number of fish engaged in other moving}) \\ + 1 (\text{number of fish milling}) \\ - 1 (\text{number of fish eddying}) \\ - 3 (\text{number of fish holding})] \\ \div (\text{number of fish visible}).$$

Other moving was not observed in Trial 1 but was in Trials 3 through 5. The particular forms of response variables (3) and (4) were selected because they represent orthogonal contrasts for linear trends among behavioral categories. Additional comparisons based on the quadratic and cubic responses were not analyzed. For both response variables (3) and (4), the higher the value, the more active were the fish.

The regression analyses used indicator (dummy) variables to adjust for trial effects related to species composition, weather, or other between-trial differences. After adjustment for trial effects, the independent variables associated with sound levels of an exposure (mean peak pressure in decibels re 1 μPa and the square of mean peak pressure in decibels re 1 μPa) were entered into the regression model to determine their association with the response variable. To assess effects of exposure levels on the vertical distribution of the fish in the enclosure, the dependent variable selected for analysis was

$$(5) \quad Y_i = \text{absolute value of the difference between the percent of visible fish in the upper two thirds of the enclosure during the exposure and preexposure periods of sound presentation } (i = 1, \dots, 16).$$

The position of the rockfish school in the water column varied with species, and changes in response variable (5) indicate sound-induced movement of the fish school either up or down in the water column. Analysis of variable (5) was based on data collected during the entire sound exposure period.

To assess effects on behavioral patterns, the percent of fish eddying and the percent of fish engaged in milling or other moving were evaluated. In both cases, the dependent variable used in the analysis was

$$(6) \quad Y_i = \text{absolute value of the difference in the percent of visible fish engaged in a behavior pattern between the exposure period and preexposure periods of a sound presentation } (i = 1, \dots, 16).$$

Changes in variable (6) indicate shifts from one behavioral category to another. Response variable (6) was analyzed using just the observations from the first 5 min of sound exposure.

Results

Sound Characterization during Trials

The weather conditions during the behavioral experiment were usually calm with a few brief periods of moderate winds. As a result, a warm surface layer was observed in the temperature profile data during most of the experimental period

(Trials 1, 3, 4, and 5). This produced downward refracting conditions as shown by sound velocity profiles, although earlier wind-driven mixing had produced a more uniform sound velocity profile for Trial 2. Detailed tabulations of the depth profiles of temperature, salinity, and sound velocity appear in Pearson et al. (1987).

The ambient acoustic noise in the Estero Bay study area (65 and 75 dB) was typical of shallow-water areas in that it was influenced primarily by wind noise (up to 94 dB at 400 Hz) and biological noise (pistol shrimp, 97 dB at 6.3 kHz) with some low-frequency contributions from sporadic small craft traffic (80 dB at 16 Hz). Radiated noise from the M/V *NAUTILUS* moving at about 5.5 kn (10.2 km/h) had dominant lines in the spectrum (127 dB from 200 to 800 Hz) from slightly cavitating propellers. Even during a fullpower backdown, noise from the M/V *NAUTILUS* (136 dB at 120 Hz) was more than 50 dB less (a factor of 0.003) than the peak pressure level at the same distance (110 m) from the air gun. Radiated noise from the F/V *BONNIE MARIETTA* moving at slow speed (estimated 3 kn or 5 km/h) showed a tonal of 103 dB at 40 Hz produced by the propeller or about 20–30 dB above the local ambient noise level.

The mean peak pressures measured at the field enclosure during each sound presentation appear in Table 2. Additional measurements were made in the enclosure for an average source distance of 50 m in order to determine the variation of peak pressure level with depth (Table 2). Generally, the pressure level decreased 4 dB for a 1.5-m decrease in depth. Examples of the observed pressure–time waveforms (i.e. air-gun signature) and their associated pressure level spectra (Fig. 2 and 3) illustrate the change from an abrupt signature to a ramped signature as the distance between the air gun and the enclosure increased. These signature changes were due to the shifts in the relative influence of bottom and surface reflections.

Description of the Behavioral Changes

The captive rockfish exhibited a number of well-defined behaviors so that we were able to tabulate the number of fish observed in different behavioral categories at each observation during control periods and sound presentations. Detailed data tabulations appear in Pearson et al. (1987).

Under control conditions, the rockfish exhibited the behavior described by Keenleyside (1979) for what he termed a relatively stationary school. The fish generally hovered or held position in the water column (holding position, Fig. 4). When a current was present, the fish oriented parallel to each other and faced into the current (holding position, directed, Fig. 4). When the current slackened or was changing direction, individuals faced in different directions (holding position, undirected, Fig. 4).

Several types of movement were observed under control conditions. Undirected movement or eddying (Fig. 4) occurred intermittently. Fish would cease holding position to move slowly around the enclosure in meandering rather than directed or circular paths. Eddying was similar to the “short radius behavior” described by Keenleyside (1979) but with continuous, smooth movement rather than jerky motions. The blue rockfish (*S. mystinus*) exhibited directed movement (Fig. 4) in which the fish oriented parallel to one another and facing into the current. The polarization of the school was maintained as individual fish inched forward into the current until they reached the enclosure wall where they would turn, swim slowly to the back of the school, reorient into the current, and begin to inch forward again. Milling (Fig. 4) has been described by Keenleyside (1979) and is a special form of schooling behavior

TABLE 2. Chronological list of test ranges and peak pressure in the behavioral experiment in Estero Bay. Sound levels are dB re 1 μ Pa. P_+ , maximum positive pressure; P_- , maximum negative pressure; P_m , effective peak pressure as defined in Equation 3 in Materials and Methods; SD, standard deviation of P_m .

Date and time	Range (m)	P_+ (dB)	P_- (dB)	P_m (dB)	SD (dB)
Trial 1					
July 14					
1136	5800	137.6	137.1	137.4	1.2
1214	2900	154.7	151.2	153.2	1.0
1303	1500	158.4	159.0	158.7	2.5
1332	760	160.9	161.4	161.2	3.1
1352	350	175.3	177.9	176.7	2.6
1429	185	178.2	178.2	178.2	1.7
Trial 2					
July 15					
0843	1760	156.2	154.7	155.5	1.3
0953	150	181.1	184.7	183.1	1.0
1053	100	187.2	184.8	186.1	0.9
1254	46	194.7	195.0	194.9	1.6
1354	59	194.8	192.0	193.5	1.0
Trial 3					
July 16					
0950	11	206.3	207.3	206.8	1.6
1126	225	175.6	176.5	176.0	1.4
Trial 4					
July 17					
0814	30	197.0	201.3	199.4	0.9
0914	51	193.0	189.6	191.5	0.8
Depth profiles					
July 17					
0940	62	190.0	187.5	188.8	3.1
0944	50	195.2	190.7	193.7	0.9
0946	47	192.1	189.2	190.7	1.0
0950	49	190.6	185.2	188.3	0.6
Trial 5					
July 18					
0816	17	203.2	206.6	205.1	2.2
0916	135	182.4	177.7	180.4	0.6
1016	65	190.3	189.0	189.7	0.8
1123	106	183.6	181.6	182.7	0.4
1230	66	189.6	186.8	188.3	1.2

in which the fish follow each other in a closed circle. Under control conditions, eddying blue rockfish would occasionally coalesce into a short-lived mill, but intense milling was observed only under sound presentation. Other moving behaviors observed under control conditions included swimming up and down through the water column and back and forth along the enclosure wall.

Behavioral Responses to Sounds from the Air Gun

The effects of sound exposure on the behavior of captive rockfish were evident as (1) shifts in the vertical distribution (either up or down), (2) shifts in behavior, and (3) the occurrence of alarm and startle responses.

Figures 5 to 8 depict the linear contrasts used to indicate changes in water column position (response variable (2)). In Fig. 5 to 8, each vertical line represents the result of the linear contrast for one observation. The longer the line below the zero point, the more fish were observed in the lower one third of the water column. The longer the line above the zero point, the more fish were observed in the upper two thirds of the water

column. Figures 9 to 12 depict the linear contrasts used to indicate shifts from holding through eddying to milling (response variable (3) for Trial 1 and response variable (4) for Trials 3, 4, and 5). In Fig. 9 to 12, the higher the line above the zero point, the more fish were observed in milling or other moving. The lower the line below zero, the more fish were observed in holding.

Plots of the percentage of rockfish in either the upper two thirds or lower one third of the field enclosure (Fig. 5 to 8) indicate shifts in vertical distribution under exposure to high sound levels relative to the preexposure observations (response variable (2)). The 176.7- and 178.2-dB exposures of Trial 1, the 206.8-dB exposure of Trial 3, the 199.4-dB exposure of Trial 4, and the 205.1-, 189.7-, and 188.3-dB exposures of Trial 5 all show substantial shifts in water column position associated with the treatment.

Similarly, plots of the time sequence of the behavioral contrasts (3) and (4) indicate definite changes in behavioral patterns under high sound exposures (Fig. 9 to 12). The 206.8-dB exposure of Trial 3, the 199.4-dB exposure of Trial 4, and the

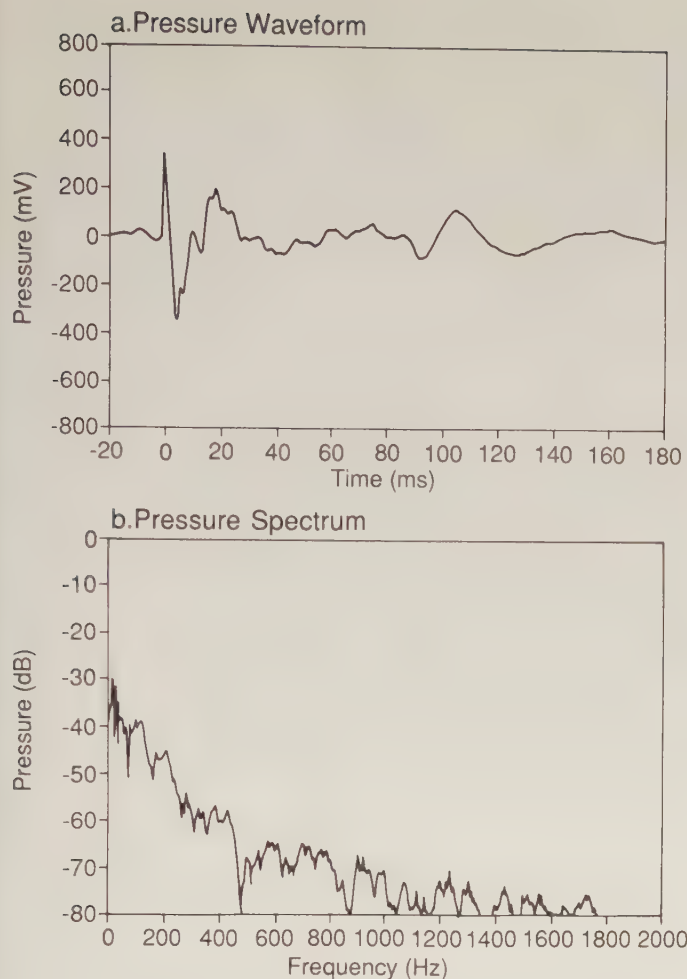


FIG. 2. Air-gun (a) pressure-time signature and (b) pressure level spectrum measured at a depth of 6 m in the enclosure for a source distance of 21 m.

205.1-dB exposure of Trial 5 show clear signs of a shift in behavior between preexposure and exposure periods. Taken together, the data in Fig. 5 to 8 suggest a general threshold of about 180 dB for alarm responses elicited by air-gun sounds.

For response variable (2) concerning shifts in vertical distribution of fish within the enclosure, regression analysis revealed a significant relationship with the maximum peak pressure level (P_m in decibels; Table 2) during exposure ($P(t_{11}) > 3.6336$) = 0.002). The percent change between control and emission periods increased significantly (Fig. 13) as the sound level increased. Utilizing the least-square fit of the response model (taking into account a weighted mean for the intercept with respect to fish group effects), an estimate of the minimum sound level to elicit a treatment effect can be estimated by setting the dependent variable equal to zero and solving for the sound level. Thus, setting $y_i = -1.64355 + 0.01015\text{dB} = 0$ yields $\text{dB} = 161.9$. Therefore, the experimental results suggest that rockfish may show changes in their vertical distribution within the enclosure at sound levels above 162 dB ($\text{CI}(151.7 < \text{dB} < 172.1)$ = 0.90).

Similar regression analysis of the percent change in milling and other moving between preexposure and exposure periods (response variable (3)) indicates a significant relationship with the level of sound exposure ($P(t_{11}) - 2.3843$) = 0.018). This relationship was not significant ($P(t_{11}) - 0.5946$) = 0.285) when data from the entire exposure period were analyzed. Similarly, a significant relationship between the absolute change in

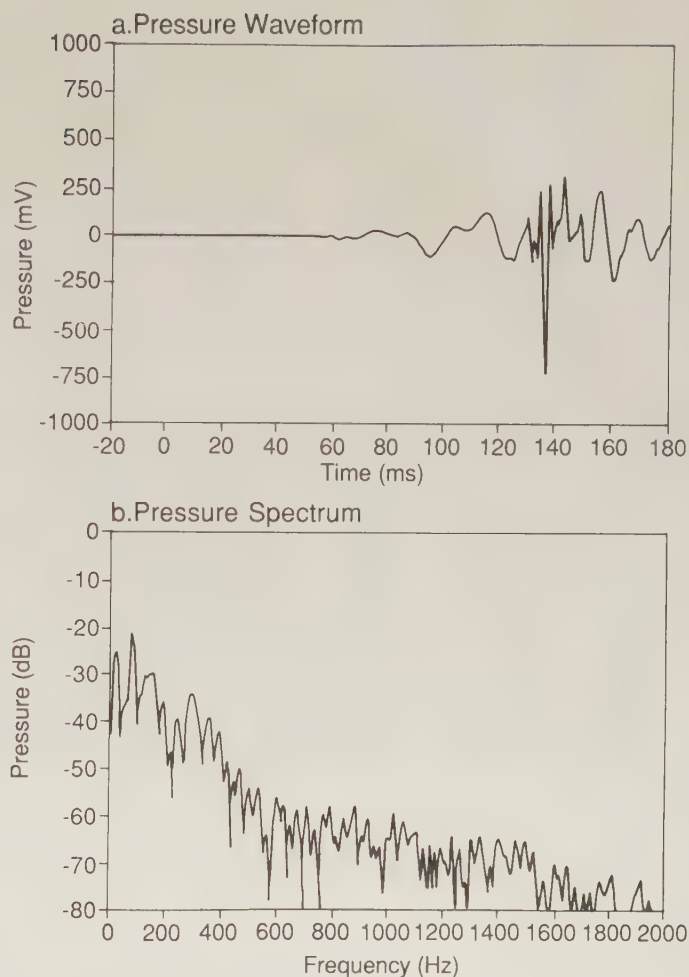


FIG. 3. Air-gun (a) pressure-time signature and (b) pressure level spectrum measured at a depth of 2.5 m in the fish enclosure for a source distance of 214 m.

percent eddying behavior and sound level was observed during the trials ($P(t_{11}) - 2.061$) = 0.032), but no significant relationship was observed between shifts in eddying behavior and sound levels based on analysis of data for the entire exposure periods ($P(t_{11}) - 0.7050$) = 0.248). Thus, rockfish increase their activity when exposed to air-gun sounds but return to preexposure behaviors within the exposure periods.

The dose-response relationships observed during the trials indicate the sound levels above which shifts in behavior patterns may become evident. From the regression relationship for milling behavior, milling would occur above an estimated sound exposure level of 167.6 dB ($\text{CI}(139.5 < \text{dB} < 194.8)$ = 0.90). Similarly, eddying behavior began to occur above a sound exposure level of 153.6 dB ($\text{CI}(128.9 < \text{dB} < 178.3)$ = 0.90). Therefore, the behavioral observations indicate that, in general, behavioral responses to air-gun sounds may be observed starting as low as 161 dB (i.e. average of 161.9 for changes in depth, 167.6 for changes in milling, and 153.6 for changes in eddying).

Alarm and Startle Responses

When exposed to air-gun sounds, black and blue rockfish responded as a school whereas vermilion and olive rockfish (*S. serranoides*) responded more individually. Under control conditions, blue and black rockfish typically formed schools

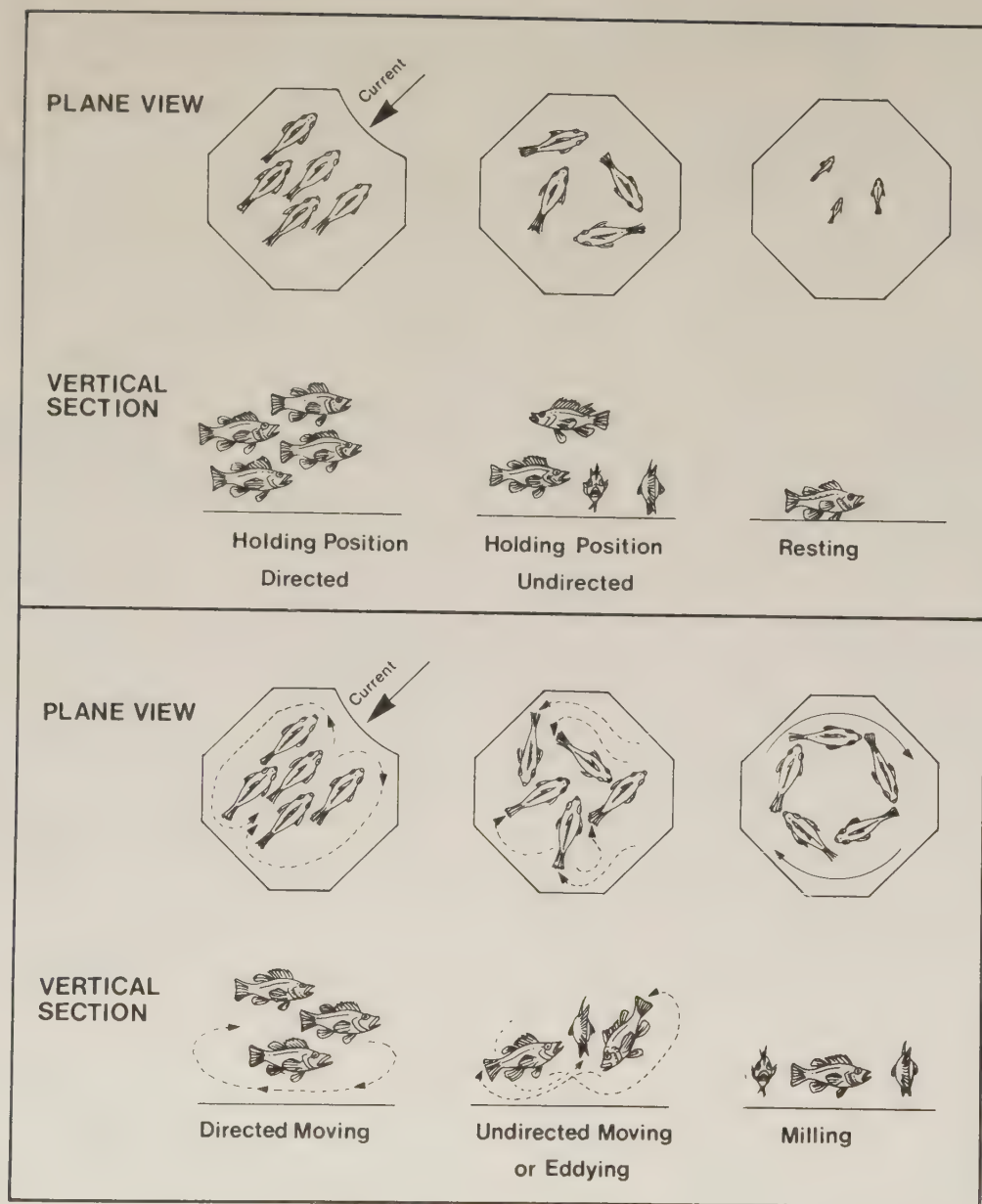


FIG. 4. Behaviors of captive rockfish in the enclosure of the behavioral experiment, May 1986.

off the bottom. Under sound exposure, blue rockfish formed a tight, rapidly circling mill, and the stationary schools of black rockfish collapsed to the bottom where they remained unpolarized and unsynchronized. Under control conditions, the vermilion and olive rockfish typically hovered at the bottom. Under sound exposure, individuals either rose in the water column and eddied at increased speed or moved closer to the bottom and became almost motionless.

Startle responses were either flexions of the body followed by rapid swimming (olive rockfish) or a series of shudders or tremors with each air-gun discharge (black rockfish). The startle responses in the olive rockfish were given to individual air-gun discharges during the first minute and resembled a Mauthner-type startle response (Blaxter et al. 1981; Schwarz and Greer 1984; Eaton and Nissano 1985). Startle responses were observed at and above 205 dB (Table 3). Except for one startle response in one black rockfish at 190 dB, none were observed at and below 199 dB. The threshold for the startle responses in olive and black rockfish appears to be between

200 and 205 dB. No startle responses were observed in vermilion or brown rockfish up to the maximum exposure of 207 dB. Blue rockfish showed no startle responses below 180 dB but were not tested above 180 dB.

Alarm responses were observed at and below the sound exposure levels where startle responses were evident (Table 3). Alarm responses in the blue and black rockfish were first observed at lower levels than those in the vermilion and olive rockfish. Alarm responses in blue and black rockfish were first observed at 177 and 180 dB, respectively. In two trials with vermilion rockfish, alarm responses were first observed at 186 and 195 dB. For olive rockfish, alarm responses were observed above 199 dB but not at 192 dB. Strong alarm responses were noted from 178 to 207 dB, the highest level tested. Alarm responses increased in occurrence and intensity as the sound intensity increases (Table 3). Although the character of the alarm response varied with the species of rockfish examined, the data in Table 3 suggest that a general threshold for behavioral responses to sounds of a single air gun was about 180 dB.

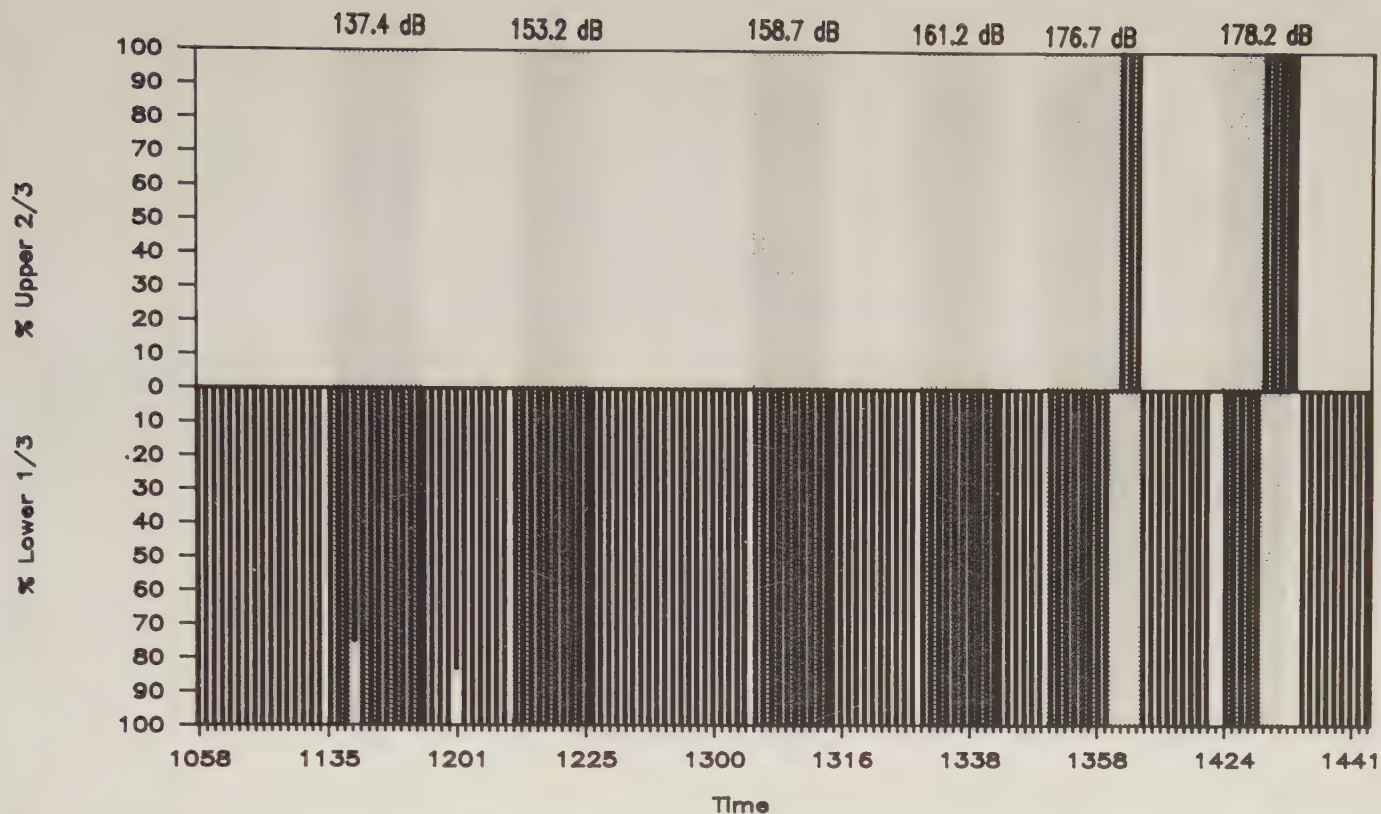


FIG. 5. Relative vertical position of rockfish in the water column of the enclosure per observation period during emission (shaded background) and nonemission (clear background) periods for Trial 1.

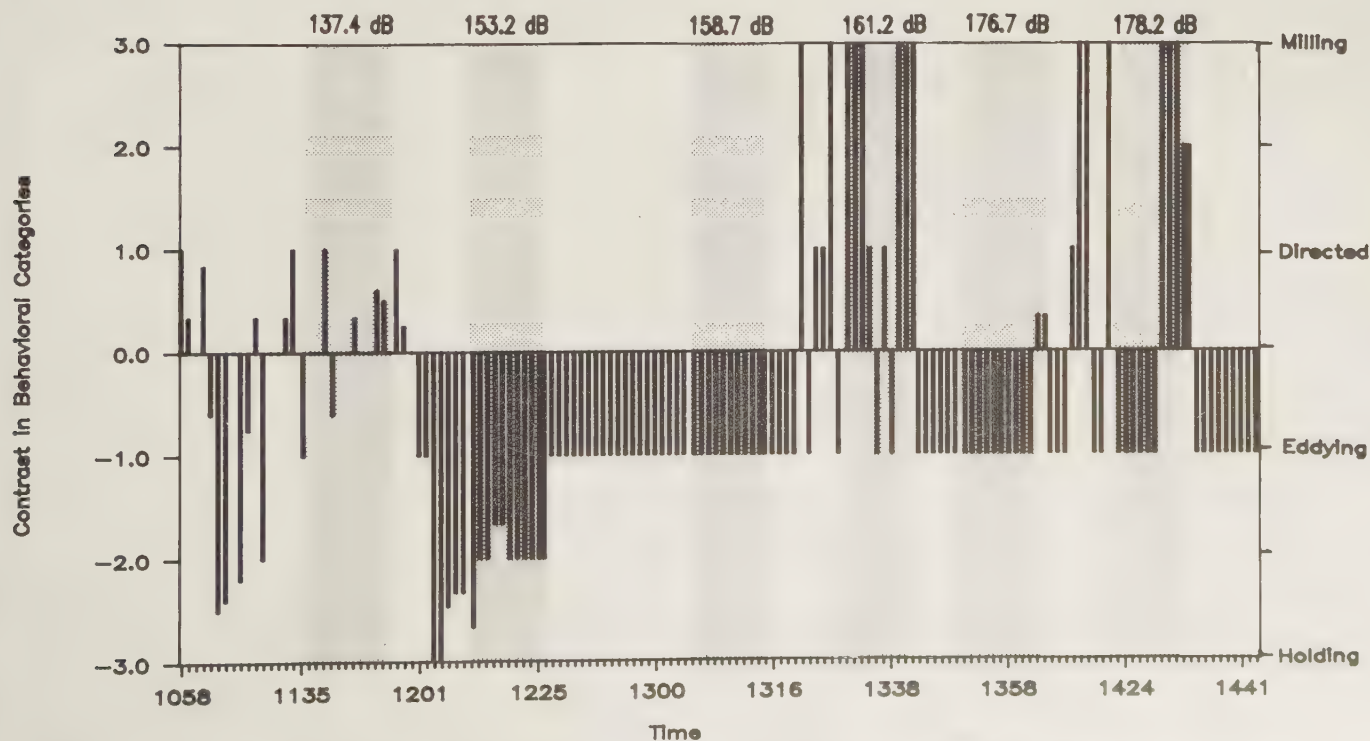


FIG. 6. Time sequence of behavioral patterns exhibited by rockfish in the enclosure as measured by linear contrast (2) for Trial 1.

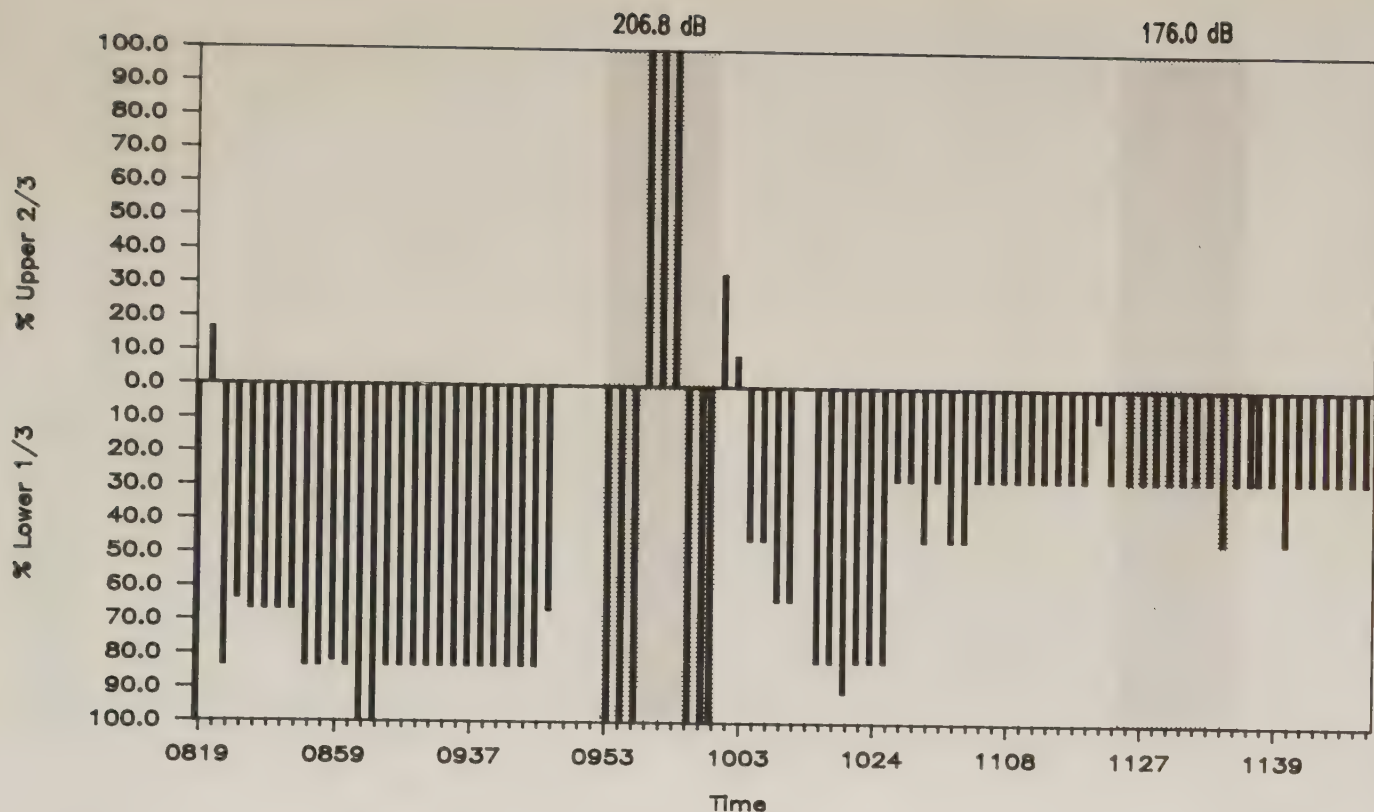


FIG. 7. Relative vertical position of rockfish in the water column of the enclosure per observation period during emission (shaded background) and nonemission (clear background) periods for Trial 3.

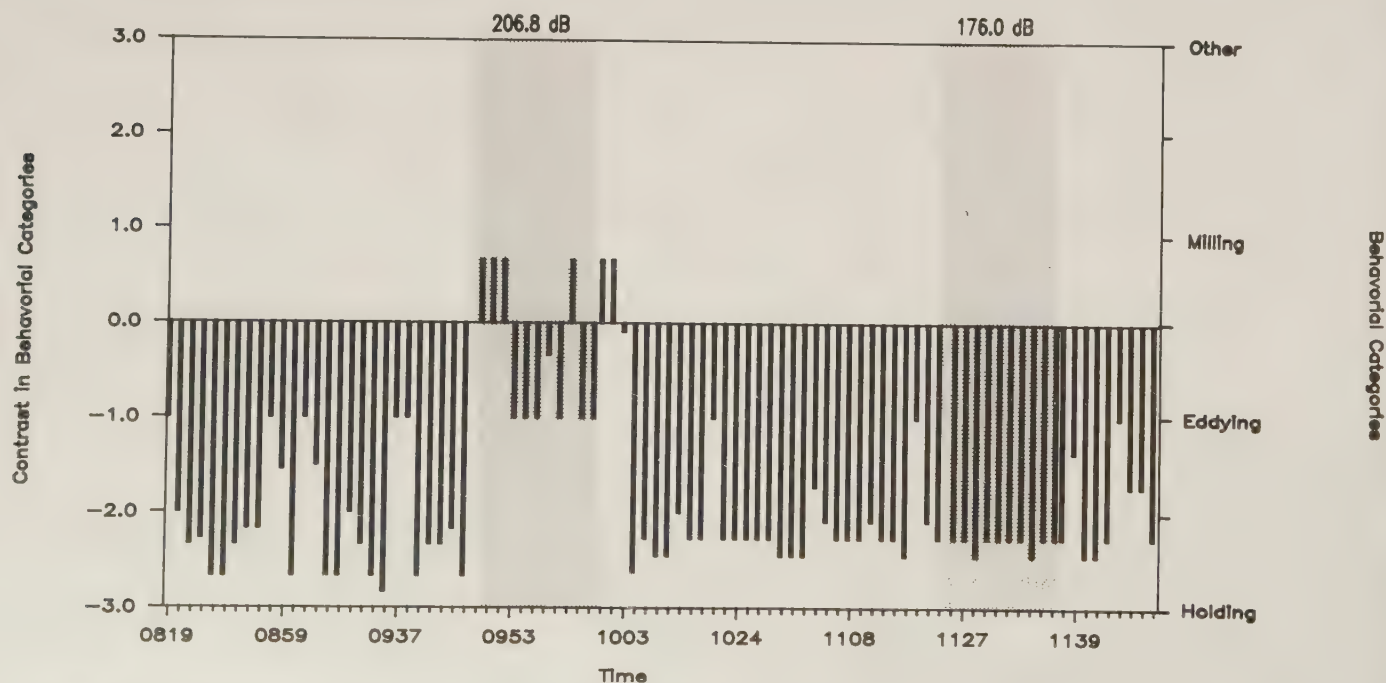


FIG. 8. Time sequence of behavioral patterns exhibited by rockfish in the enclosure as measured by linear contrast (3) for Trial 3.

Discussion

The behavioral experiment clearly showed that several rockfish species react to air-gun sounds with alarm and startle responses, but that the character and extent of such responses differ with species and sound level. Avoidance and other more subtle behavioral responses may occur, but the limitations of

the experimental enclosure would have prevented their expression. Our behavioral observations alone cannot confirm or deny the existence of avoidance.

The alarm responses observed here appear to be extensions of behaviors typically seen or expected in escape from predators. Tight mills and "flash expansions" or loss of polarization have been observed for schools under attack by predators

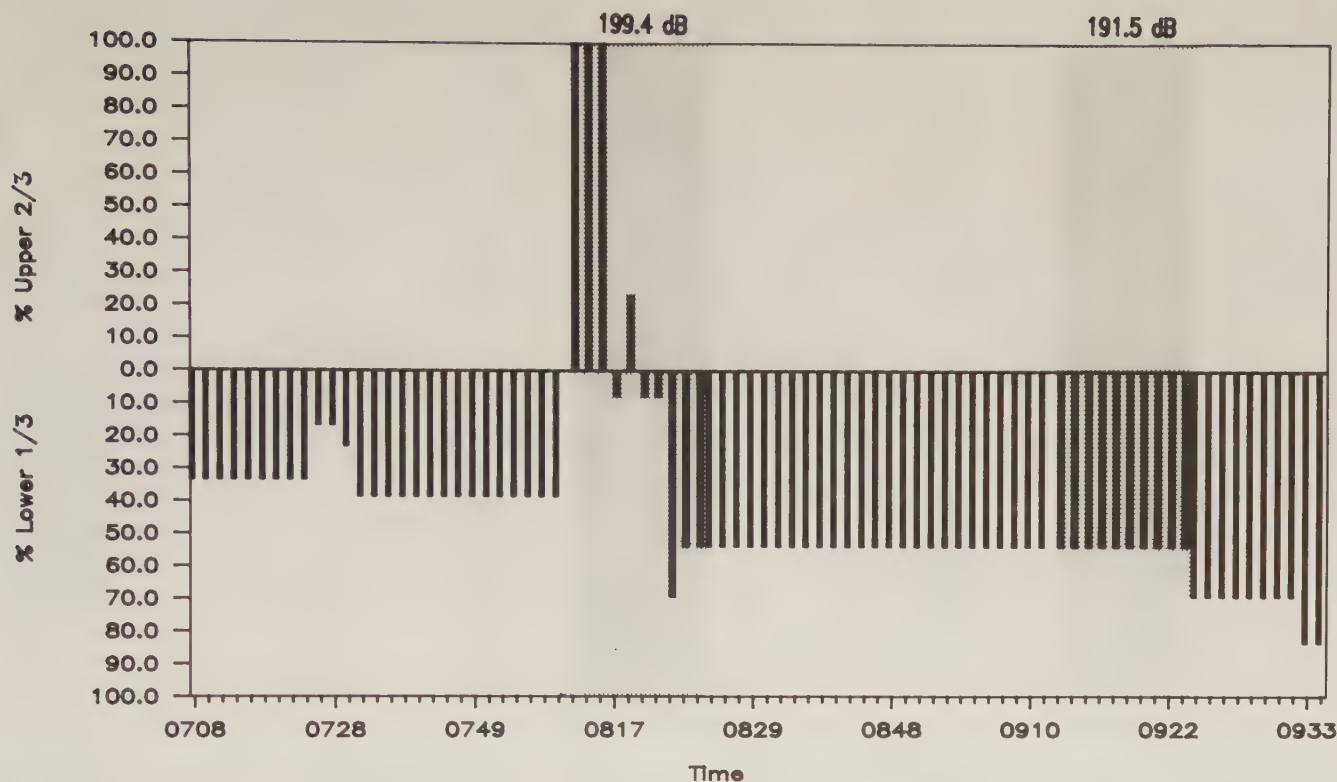


FIG. 9. Relative vertical position of rockfish in the water column of the enclosure per observation period during emission (shaded background) and nonemission (clear background) periods for Trial 4.

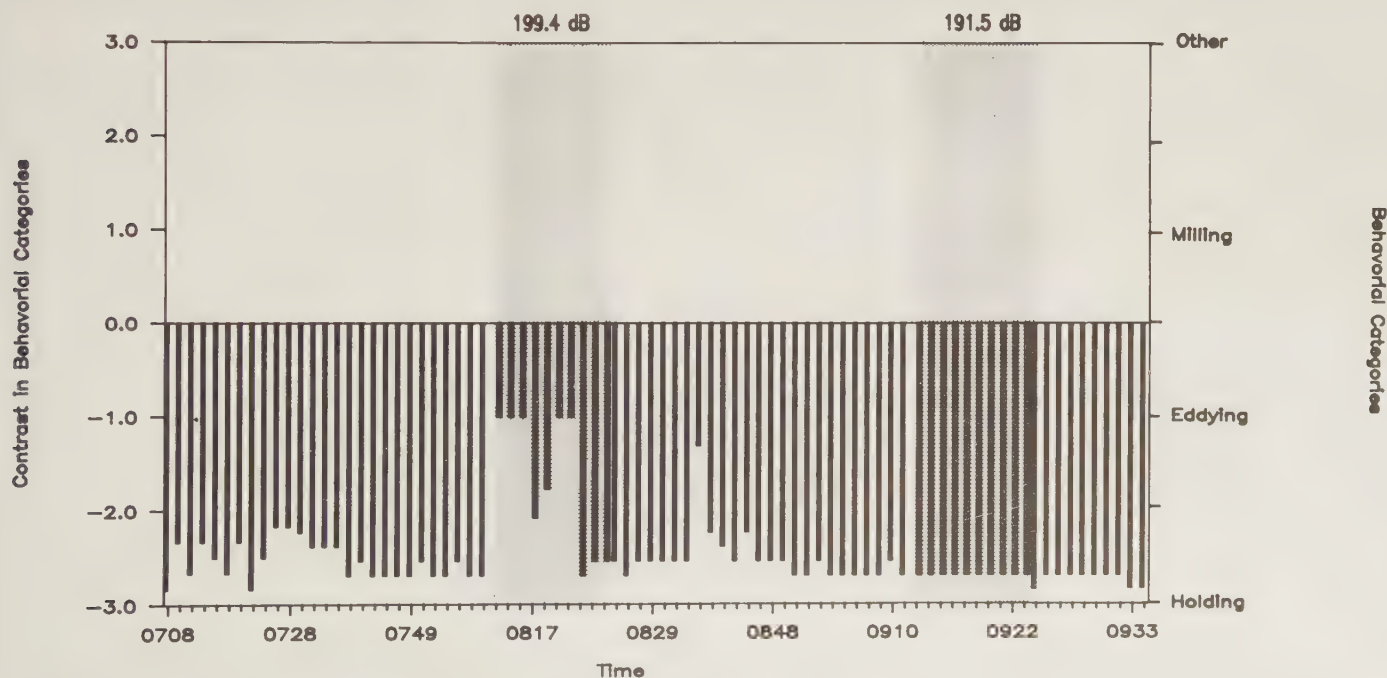


FIG. 10. Time sequence of behavioral patterns exhibited by rockfish in the enclosure as measured by linear contrast (3) for Trial 4.

(Keenleyside 1979), so that terming the changes in schooling behavior observed in blue and black rockfish an alarm response is supported somewhat by the ethological literature.

The threshold for startle responses was between 200 and 205 dB; however, because of the nature of the sound signatures at the enclosure, startle responses may be elicited at different levels or under limited circumstances during actual geophysical operations. At short range between the sound source and enclosure,

the signature of the air-gun sounds had the abrupt character that Blaxter et al. (1981) considered most likely to elicit startle responses (Fig. 2). At longer ranges during the experiment (214 m; see Fig. 3), the sound levels were, of course, lower, but because of interaction with the sea surface, the sound signature had also changed character from abrupt to ramped. If an abrupt signature is necessary to elicit a startle response, then startle responses might occur at lower sound levels, when an

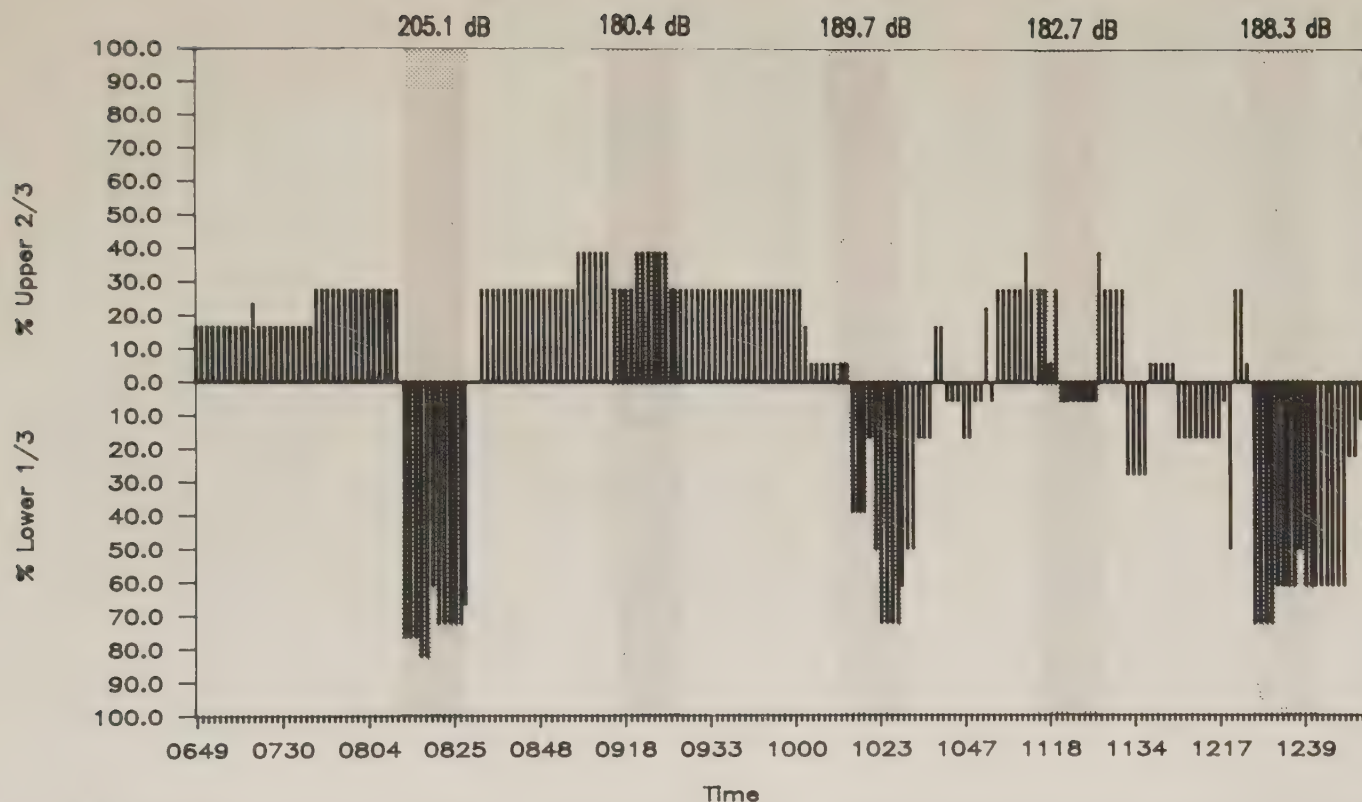


FIG. 11. Relative vertical position of rockfish in the water column of the enclosure per observation period during emission (shaded background) and nonemission (clear background) periods for Trial 5.

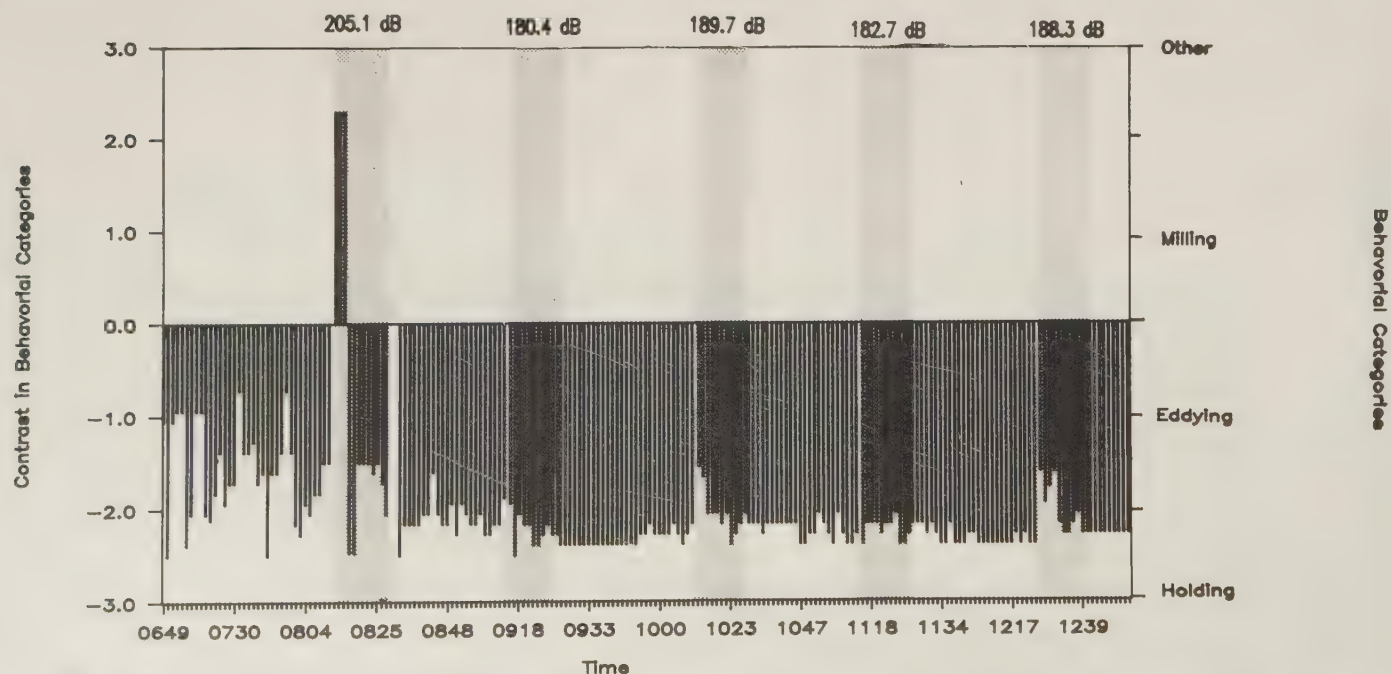


FIG. 12. Time sequence of behavioural patterns exhibited by rockfish in the enclosure as measured by linear contrast (3) for Trial 5.

abrupt signature is present, than we observed. Also, the acoustic signature of air-gun arrays presented by Malme et al. (1986) shows an instantaneous rise to maximum intensity when the receptor is on the beam axis. Off-axis sounds have the ramped pattern. Therefore, when survey vessels are running tracklines, the signature changes from ramped to abrupt and back to ramped as the vessel passes the point of interest. Under survey opera-

tions, then, the signatures most likely to elicit startle responses are present intermittently rather than continuously.

The data suggest the general threshold for alarm response to be about 180 dB. The regression analyses of the changes in depth distribution and the extent of active behaviors such as eddying and milling show that changes in these behaviors became more extensive as sound level increased. Extrapolation

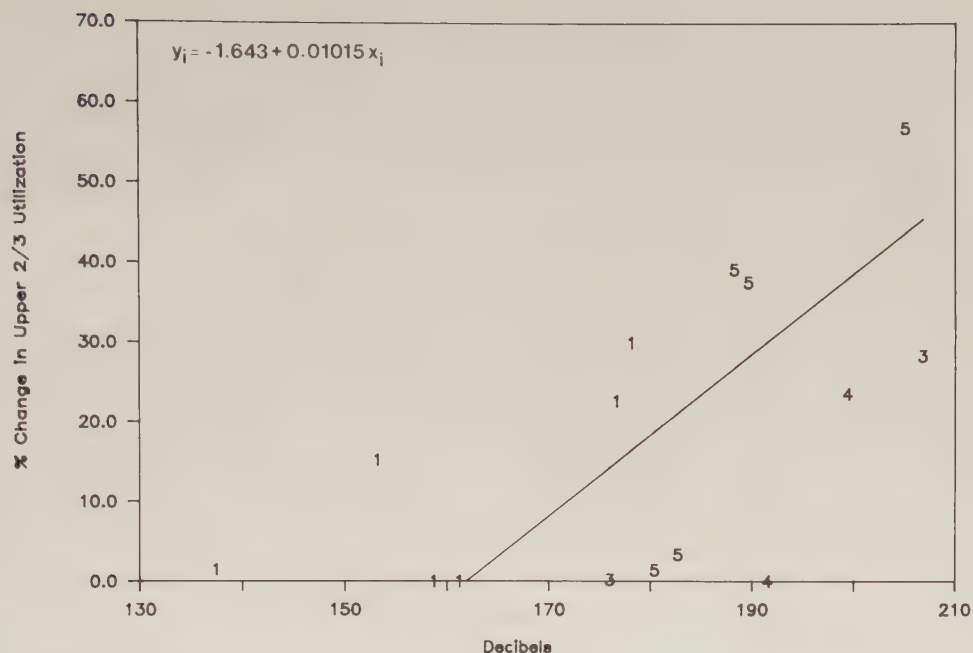


FIG. 13. Relationship between sound level (dB) of acoustic exposure and the percent shift in utilization of the upper two thirds of the enclosure (response variable (4)).

TABLE 3. Alarm (Al) and startle (St) response scores for captive rockfish presented with air-gun sounds. Sound levels are dB re 1 μ Pa. Response scores: 0, no response; 1/2, one or two fish respond; 1, several fish respond; 2, up to half the fish respond; 3, more than half the fish respond.

Sound level	Trial										Overall	
	1		2		3		4		5			
	Al	St	Al	St	Al	St	Al	St	Al	St	Al	St
207					3	3	3				3	3
205									3	3	3	3
199							3	0			3	0
195			2	0							2	0
192							0	0			0	0
190									3	1/2	3	1/2
188									3	0	3	0
186			1/2	0							1/2	0
183			0	0					1/2	0	1/2	0
180									1/2	0	1/2	0
178	3	0									3	0
177	1/2	0									1/2	0
176					0	0					0	0
161	0	0									0	0
159	0	0									0	0
155			0	0							0	0
153	0	0									0	0
137	0	0									0	0
No. of fish/ trial	20		3		13		13		15			

of these regressions suggests that more subtle changes in behavior could begin as low as 161 dB.

The general threshold of 180 dB observed here agrees well with some field observations of avoidance of air-gun sounds. Discharges of a single air gun with a source level of 220 dB have been reported to change the depth distribution of whiting (Chapman and Hawkins 1969). Using the echosounder of a vessel stationed over a school of whiting, these authors observed that upon discharge of an air gun, the whiting distributed between 27 and 55 m abruptly descended and formed a com-

pact band just below 55 m. Assuming a transmission loss of $25 \log(R)$, these findings suggest that the whiting avoided sound levels above 178 dB.

The thresholds observed here indicate that startle and alarm responses could be elicited by sounds from actual survey operations. For a typical air-gun array of 65 550 cm³ with 32 guns and source level of 255 dB, the sound exposure from a trackline passing directly over a point at a depth of 100 m can be calculated from the sonar equation $S = SL - 20 \log(R)$, where S = sound level at the point, SL = source level, which here

is 255 dB, R = the range (metres), and $20 \log(R)$ is the transmission loss. For a single trackline passing directly overhead and assuming a typical vessel speed (11 km/h) and array discharge rate (6 discharges/min), a point at 100-m depth would receive sounds with abrupt signatures and levels above 180 dB from approximately 1840 discharges over a period of about 5.1 h. Similarly, a point would receive sounds above 205 dB from approximately 103 discharges over about 17 min. With the array directly overhead, maximum sound level at 100-m depth would be 215 dB. For a transmission loss of $20 \log(R)$, the distance from a 255-dB array where sound levels would be above the 205- and 180-dB thresholds for startle and alarm responses would be about 316 m and 5.6 km, respectively. For a transmission loss of $35 \log(R)$, a value more typical of shallow water, the effective distances would be 1 m for startle responses and 139 m for alarm responses. For the coastal waters of California, transmission losses 20 – $25 \log(R)$ have been observed. These calculations indicate that the conditions eliciting alarm responses are much more likely than those eliciting startle responses.

One aim of the behavioral experiment was to provide data to establish the sound exposure level in the subsequent fishing experiment (Pearson et al. 1987; Skalski et al. 1992). During this fishing experiment, sound levels at the bottom were always above 180 dB and often above 190 dB, so that the treatment level applied to the rockfish aggregations was within the range that produced the alarm responses observed here. The rockfish aggregations of the fishing experiment were probably rarely exposed to sound levels above 200 dB, the level at which startle responses were observed. The fishing experiment demonstrated a significant 52.4% reduction in catch-per-unit-effort (CPUE) in hook-and-line fishing targeted on rockfish aggregations under sounds from a single air gun producing the sound levels observed here to elicit alarm responses.

Results of the two experiments suggest that the reduction in CPUE was due to behavioral responses by rockfish to air-gun sounds. The sound levels during the fishing experiment were above those producing alarm responses but probably not above those producing startle responses. Echosounder transects of the rockfish aggregations before and during sound exposure showed that the height but not the area of the aggregation changed under sound exposure. This change in height but not area implies that the rockfish higher in the water column decreased depth to avoid the sound but did not disperse from pinnacle. Therefore, the sounds from the survey device appear to have acted mainly to reduce responsiveness to baited hooks.

While the likelihood of behavioral responses and reduced catchability is clear from the results here and in Skalski et al. (1992), how long reduced catchability might last was not addressed in our experimental design. The observation that rockfish returned to preexposure behaviors either late in the exposure period or within minutes after exposure ceased is evidence for habituation to the air-gun sounds. Because alarm and startle responses are usually not sustained long after removal of the effective stimulus, the reduced catchability can be expected to be transient. Other studies of different design are needed to know how transient any reduced catchability might be. Our study design did not address the effects of duration on the behavioral responses or catchability. In actual surveys, the survey vessel conducts 24-h/d operations for perhaps several weeks. Any other studies should include efforts to determine the influence of duration on the extent of effect and the time course of recovery.

Acknowledgements

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Effects of Sounds from a Geophysical Survey Device on Catch-per-Unit-Effort in a Hook-and-Line Fishery for Rockfish (*Sebastes* spp.)

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We examined the concern of commercial fishermen that the sounds generated by acoustic geophysical survey devices result in decreased commercial catches. In blind experimental trials, a test of effects was performed on the rockfish (*Sebastes* spp.) hook-and-line fishery located along the central California coast. A single 1639-cm³ air gun with a source level of 223 dB re 1 μ Pa was used to produce peak pressures above 186 dB re 1 μ Pa at the base of rockfish aggregations. There was an average decline in catch-per-unit-effort of -52.4% (90% confidence interval -27.9%, -76.9%) under emission conditions relative to control trials. This overall decline was also reflected in the individual catches of chilipepper (*S. goodei* ($\alpha = 0.046$)), bocaccio (*S. paucispinis* ($\alpha = 0.007$)), and greenspotted rockfish (*S. chlorostictus* ($\alpha = 0.021$)). The overall reduction in catch translated to an average economic loss of 49.8% (90% confidence interval -21.7%, -77.9%) under the test conditions of this experiment. Fathometer recordings during the study showed no significant change in an index of aggregation size as the result of air-gun emissions ($\alpha = 0.374$). However, aggregation height appeared to change as the result of emission ($\alpha = 0.094$) after adjustment for species composition of the catch.

Nous avons étudié les plaintes formulées par les pêcheurs commerciaux et selon lesquelles les sons produits par les appareils acoustiques utilisés au cours des levés géophysiques donnaient lieu à une baisse des prises. Des essais à l'aveugle ont été réalisés. Ces essais ont porté sur la pêche à la ligne du sébaste (*Sebastes* spp.) le long de la côte du centre de la Californie. Un canon à air comprimé de 1 639 cm³ et d'une puissance sonore à la source de 223 dB à 1 μ Pa a été utilisé pour produire des pressions de pointe de plus de 186 dB à 1 μ Pa à la base des concentrations de poisson. Il y a eu baisse moyenne de 52,4 % (intervalle de confiance à 90 % de 27,9 à 76,9 %) des prises par unité d'effort de pêche par rapport aux essais témoins. Cette baisse générale s'est aussi reflétée sur les prises de sébaste de Goode (*S. goodei*, $\alpha = 0,046$), de bocaccio (*S. paucispinis*, $\alpha = 0,007$) et de sébaste à tache verte (*S. chlorostictus*, $\alpha = 0,021$). La réduction totale des prises, dans les conditions des essais, a donné lieu à une perte économique moyenne de 49,8 % (intervalle de confiance à 90 % de 21,7 à 77,9 %). Des enregistrements à l'échosondeur n'ont pas permis de noter de modification significative d'un indice des tailles de concentration pendant les essais ($\alpha = 0,374$). Il semble cependant que la hauteur des concentrations, après correction pour la composition spécifique des prises, ait été modifiée par les émissions sonores ($\alpha = 0,094$).

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There has been concern that sounds generated by air guns and other acoustic devices used in offshore oil and gas exploration have been affecting the commercial hook-and-line fishery for rockfish (*Sebastes* spp.) along the California coast. Fish are known to show behavioral responses to a variety of sounds (for review, see Tavalga et al. 1981). Air-gun discharges have been reported to change the depth distribution of whiting (Chapman and Hawkins 1969). A Norwegian study suggested that fish distribution can be changed along transects made by a survey vessel using an array of air guns (Dalen and Raknes 1985). Also, a previous study in California (Greene 1985) suggested that the behavior and catchability of rockfish were affected by sounds from an air-gun array. The purpose of this study was to examine the proposition that geophysical

seismic devices can reduce the catch-per-unit-effort (CPUE) of a fishery.

A test of effects on CPUE was the primary focus of the fishing experiment reported here. An ancillary objective of this experiment was to assess the effects of acoustic emissions on the size and configuration of the rockfish aggregations. Any changes in the spatial pattern would indicate possible effects on the fishery uncluttered by the complications of fishing success.

The study was structured to deal with two problems. The first problem was the difficulty of detecting differences in fishing success when the parameter that measures success (CPUE) was known to have a high variation. A preliminary survey gathered information on the variability of CPUE in the hook-and-

TABLE 1. Power ($1 - \beta$) of the proposed field experiment to detect a 30 or 50% reduction in CPUE at a statistical significance level of $\alpha = 0.10$ as a function of the number of control (n_C) and emission (n_E) trials.

Number of trials ($n_C = n_E$)	Power	
	$\Delta = 30\%$	$\Delta = 50\%$
14	0.39	0.74
20	0.46	0.84
26	0.52	0.90

line fishery in order to calculate the necessary sample size for the fishing experiment. The second problem was the difficulty of attributing any observed effects to sounds from seismic survey activity. Because an experimental approach permits designs that actively control for confounding factors, systematic errors, and alternative explanations (Cox 1958), an experimental approach was adopted.

Preceding the fishing experiment discussed here, a behavioral experiment (companion paper, Pearson et al. 1992) determined the threshold at which sounds from an air gun produced a startle response or other behavioral changes in captured rockfish. Output from this behavioral experiment was used to establish test parameters of this fishing experiment. Specifically, the behavioral data were used to examine the appropriate magnitude of the experimental sound treatment and the minimum distance to be traveled between trials to assure statistical independence of the trials.

Experimental Design and Methods

Preliminary Survey

A preliminary survey was conducted May 6–10, 1986, to select a standard unit of effort and estimate associated variance components for sample size calculations. A total of 17 fishing trials was performed on separate rockfish aggregations. Each setline consisted of 80 hooks spaced 0.305 m apart and baited with salted mackerel. We deployed one to four setlines per trial, each with a bottom time of either 15 or 20 min. Based on industry procedures and statistical performance, a standard unit of effort consisting of a fishing trial with three setline deployments and bottom times of 20 min was ultimately selected for the field experiment. The preliminary survey produced a mean CPUE of 62.5 fish per trial and a between-trials coefficient of variation (CV) of 95.7%.

To establish the level of replication required to detect a significant effect during the fishing experiment, sample size (n) calculations were performed using noncentral F -distributions (Tiku 1967, 1972). Ideally, in a situation where the consequences of falsely identifying an acoustic effect are equal to missing an appreciable effect (e.g. 50% reduction in CPUE, $\Delta = 0.50$) on the fisheries, the Type I (α) and Type II (β) error rates should be equal. The magnitude of the treatment effect (Δ) was expressed as a function of the control (μ_C) and emission (μ_E) means where $\Delta = |\mu_E - \mu_C|/\mu_C$. An α -level of 0.10 for a one-tailed test of the null hypothesis of no effect under acoustic emissions was chosen for this study to bring about a closer equality of these error rates. With $n = 20$ replicate trials per treatment (Table 1), the fishing experiment had a projected power of $1 - \beta = 0.84$ in detecting a 50% decline in CPUE at a statistical significance level of $\alpha = 0.10$. This level of

fishing effort ($n = 20$) and set of quantitative objectives ($\alpha = 0.10$, $\beta = 0.16$, and $\Delta = 0.50$) were selected for the fishing experiment. As it turned out, the preliminary estimates and stipulations ($\Delta = 0.50$, CV = 95.7%) used in the power calculations closely approximated the actual parameters observed during the field experiment (i.e. $\Delta = 0.524$ and CV = 72.4% for controls, CV = 92.5% for emission trials).

Fishing Experiment

Study area

The fishing experiment was conducted from July 19 to August 3, 1986, off the California coast (Fig. 1) north of Morro Bay between Pt. Piedras Blancas and Pt. Sur where there is a productive commercial hook-and-line fishery for rockfish. All fishing trials were restricted to fish aggregations on rock pinnacles occurring at depths between 82.3 and 182.9 m. The minimum distance between successive trials was 10 km apart. A distance of 10 km was selected to assure that fish aggregations were not exposed to a sound level greater than 170 dB re 1 μ Pa radiating from a previous test location (hereafter, dB will be expressed as relative to a reference level of 1 μ Pa). Based on preliminary results from a behavioral experiment (Pearson et al. 1992), sound levels below 170 dB were not expected to influence fish behavior. A minimum of 3 d was allowed before a repeat control or emission trial in the same area. For statistical independence, a unique rock pinnacle was used for each trial of the fishing experiment.

Experimental design

The field experiment used a completely randomized design with individual fish aggregations being the experimental units. The treatments, which were randomized to the trial sequence, consisted of two acoustic emission levels, zero or mock emission, and acoustic emission above 180 dB at the base of the rock pinnacle. The 180-dB level was selected because the behavioral experiment (Pearson et al. 1992) indicated that levels above 180 dB elicit behavioral responses in rockfish. Knowledge of the treatment regime was limited to the project biometrician with the acoustic crew being informed only after all sound production equipment had been deployed. With only a single air gun, it was also possible to keep the fishing crew blind to the treatments during the study.

A source of high-pressure air was used during the control trials to simulate the bubbles released during air-gun operation. This mock or control emission was done to eliminate possible bias from visual cuing of the fishing vessel operators when the air gun was operating. A solenoid valve air control system enabled selection of either air gun or bubble source from the control panel. It was found that a 1-s burst of high-pressure air through a perforated tube located near the air gun provided a bubble at the surface that was similar in size to the bubble produced by the air-gun operation. This system was operated at the same rate of six pulses per minute as the firing of an air gun during acoustic trials. Acoustic monitoring during the trials showed that the pulsing of the bubble source had no acoustic influence on the control trials.

Fishing trials were performed using a 11.6-m fishing vessel, the F/V *BONNIE MARIETTA*. A fishing trial began with three echosounder transects using a Si-Tex model HE-351 echosounder to measure the size and configuration of the fish aggregation selected. The aggregations recorded on the chart recordings were analyzed with a Planix 6 digital planimeter to measure the area of each aggregation in square centimetres. The height of the aggregation on the chart recording was measured

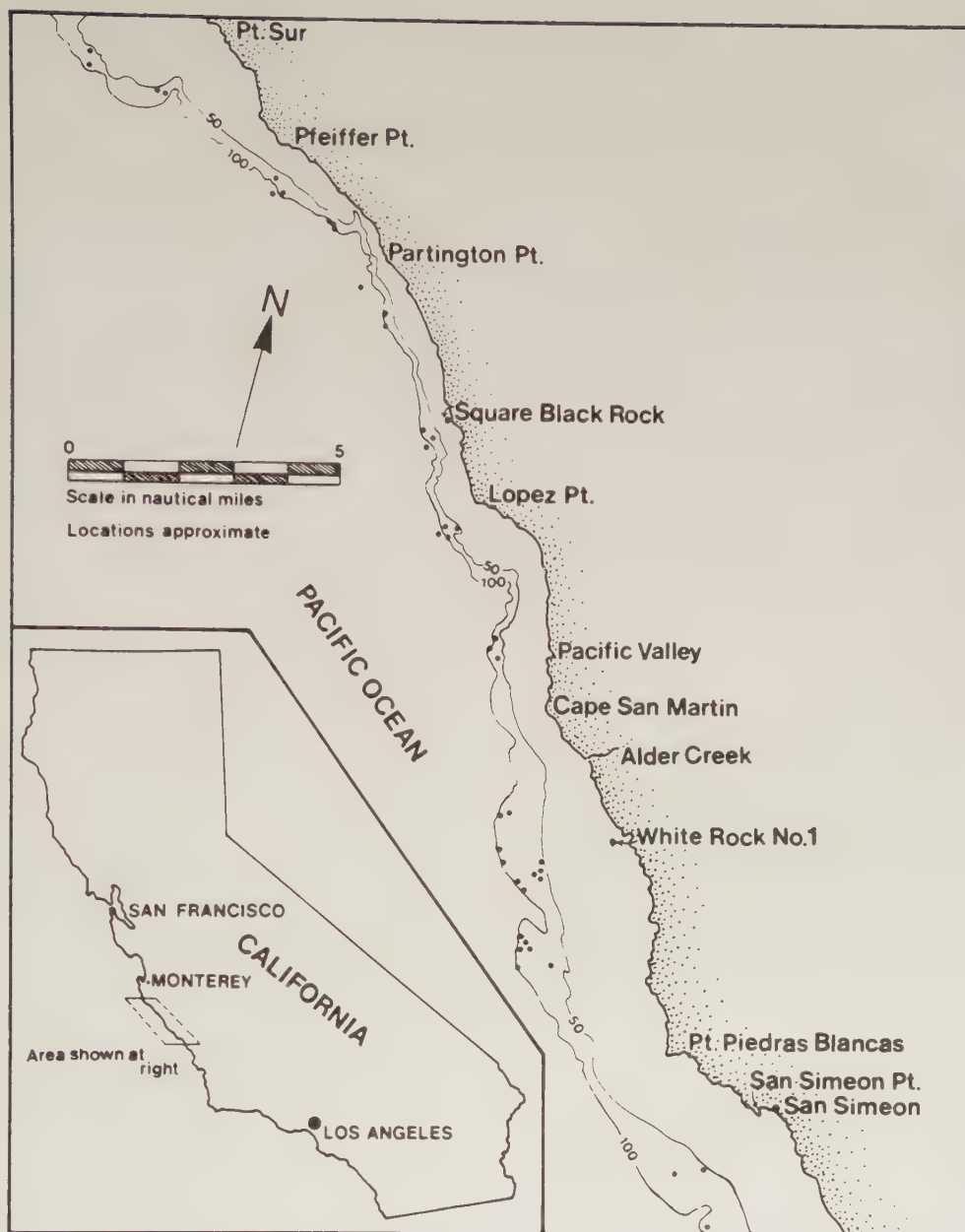


FIG. 1. Locations of the fishing trials (dots) along the California coast used in the fishing experiment.

in millimetres. A mean was calculated from two replicate measurements of aggregation area and height for each record.

After completion of the three preoperational transects, the 33.5-m industrial vessel M/V *NAUTILUS* was instructed to commence the scheduled treatment. The M/V *NAUTILUS* began its treatment maneuvers by traversing over the top of the rockfish aggregation and then proceeding to a standoff distance of approximately 165 m where it continued circling the pinnacle throughout the course of the trial to provide sound exposure during fishing. The passage over the aggregation was performed to provide an initial sound exposure of at least 180 dB. During the fishing experiment, sound levels at the sea bottom were always above 180 dB and often above 190 dB, so that the treatment applied to the aggregation was within the range that produced alarm responses in the behavioral experiment. The aggregations were exposed to a lesser extent to sound levels above 200 dB, the level at which startle responses were observed. The standoff distance was chosen to be the minimum

distance that could be accommodated without the sound vessel (i.e. the M/V *NAUTILUS*) interfering with the fishing vessel F/V *BONNIE MARIETTA*. After the passage of the sound boat over the aggregation, the fishing vessel deployed the first setline and repeated the three echosounder transects. A sequence of three setlines was deployed with one setline soaked at a time. A trial ended with the retrieval of the third setline.

The standard unit of fishing effort used in the trials of the fishing experiment was three setlines deployed for 20 min each. Each setline had 80 hooks spaced 0.305 m apart and baited with salted mackerel as used in the preliminary survey. Various colored rubber balloons were added to the hooks as an additional lure to the rockfish and to hide the hook's shank. The hooks on the setline were numbered individually from 1 to 80 to record fish placement along the line. All trials consisted of three setlines regardless of the fishing success on earlier lines.

On recovery of the setlines, the catch was examined and the species and size category recorded by hook location. Fish

caught during a fishing trial but detached from the setlines during recovery (i.e. "floaters") were also recorded by species and size category for assignment to the proper setline. Floaters were included in the data analyses. Fish were sorted according to market value (i.e. whole fish or fillet fish species), placed in fish baskets, and weighed on a deck scale after completion of each trial. The CPUE for a trial was calculated as the number of fish caught during the three setlines.

Species composition of a rockfish catch, as well as the catch weight, was used to determine the economic value of a particular catch to the fishermen. For each trial, the total weight of fillet fish (e.g., chilipepper (*S. goodei*), bocaccio (*S. paucispinis*), and yellowtail rockfish (*S. flavidus*)) and of fish sold whole in the marketplace (e.g. vermilion (*S. miniatus*) and greenspotted (*S. chlorostictus*) rockfish) was measured. Prices paid to the fishermen at the time of this study were \$1.98/kg for whole fish and \$.99/kg for fillet fish. Using these prices, cash value of the catch for each trial was computed. It is important to note that results of the data analysis on the cash value of catch is invariant to the actual prices received by fishermen so long as the ratio of the wholesale price of whole to fillet species remains 2:1.

Sound production and monitoring

The same sound production system was used in this fishing experiment as was used in the behavioral experiment (Pearson et al. 1992). A single 1639-cm³ air gun operated at 4500 psi (1 psi = 6.895 kPa) was chosen in order to provide a simple, well-defined sound source for the field trials. Air guns are the type of device most frequently used in geophysical surveys off California (Malme et al. 1986). During experimental fishing, the air gun was towed at a depth of 6.1 m and a speed of about 1.8 km/h. The towing depth was typical of industry practice. The towing speed was slower than industry practice so that the sound boat had sufficient maneuverability at the pinnacle to deliver the experimental treatment levels desired. A diesel-driven air compressor on the M/V NAUTILUS provided high-pressure air in sufficient volume to operate the air gun at a firing rate of six pulses per minute during the fishing trials. The compressor was mounted on vibration isolation supports to reduce sound radiation into the water.

The sound monitoring and analysis systems were installed on the M/V NAUTILUS. A hydrophone towed 12 m behind the air gun provided data for determining the acoustic source level of the gun and monitoring its output during the course of each trial. The signals from the hydrophones were amplified and recorded on a multichannel analog tape recorder, a storage oscilloscope, and a strip chart recorder. A real-time narrow-band spectrum analyzer was also used to obtain records of pressure wave forms and pressure level spectra. All equipment were calibrated to give pressure sensitivity with a reference of 1 V/ μ Pa. Spectrum analysis records were calibrated to obtain the sound pressure levels in a specified analysis bandwidth (termed band level (BL)) or in a 1-Hz bandwidth (termed spectrum level (SL)) relative to 1 μ Pa. Details of the acoustic measurement technique can be found in Pearson et al. (1987).

Statistical analysis

The analyses of CPUE, cash value of the catch, and spatial configuration of the rockfish aggregations are not wholly independent (e.g. cash value is a function of catch) but were deemed important either in exploring alternative response variables for measuring the effects on the fishery or in assessing the economic consequences of any observed effects. Throughout, sta-

tistical significance will imply an α -level of 0.10 or less. Exact α -levels are also reported for each statistical test performed.

Covariance analysis was used to analyze the total catch of all rockfish and the catches of the five most abundant species: chilipepper, vermilion rockfish, bocaccio yellowtail rockfish, and greenspotted rockfish. The variable $\ln(\text{catch} + 1)$ was used as the dependent variable with catch being the number of fish. The logarithmic transformation was performed to stabilize the within-treatment variances and was appropriate because (1) the CV was constant across treatments (Snedecor and Cochran 1980, 291–292; Sokal and Rohlf 1981; Bliss 1967, p. 232), (2) proportional rather than additive effects were expected (Snedecor and Cochran 1980, p. 291–292), and (3) the catch showed positive skewness (Sokal and Rohlf 1981, p. 419–421). The addition of 1 to all data enabled analysis of trials with zero catch. Polynomial response equations to degree 3 (i.e. linear, quadratic, or cubic) were fitted to the catch data as a function of depth for all individual species, as well as total catch. Stepwise regression procedures were used to determine the degree of the polynomial equations. In addition, the height and area of the rockfish aggregation were used in the covariance analysis. One-tailed tests of the null hypotheses of no difference in mean CPUE or cash value against the alternative of a decline in response were performed.

The relative change (RC) in CPUE and the cash value of the catch as the result of the acoustic emissions of the air gun were estimated by the equation

$$(1) \quad \hat{RC} = \frac{\bar{x}_E - \bar{x}_C}{\bar{x}_C}$$

with associated estimate of variance

$$(2) \quad \hat{Var}(\hat{RC}) = \left(\frac{\bar{x}_E}{\bar{x}_C} \right)^2 \left[\frac{S_{x_E}^2}{\bar{x}_E^2} + \frac{S_{x_C}^2}{\bar{x}_C^2} \right]$$

where $\bar{x}$ and s^2 are the sample mean and variance among replicate trials for control (C) and emission (E) conditions, respectively. Construction of 90% confidence interval estimates for RC was based on the formula $\hat{RC} \pm 1.645 \sqrt{\hat{Var}(\hat{RC})}$.

Regression diagnostics were performed as part of the data analysis to identify influential data and outliers. Studentized residuals were calculated to identify influential data points with high leverage (Belsley et al. 1980, p. 17–20), but in no instance was the α -level for a residual test less than $\alpha = 0.348$. Additionally, leverage points were analyzed by data-point deletion techniques (Belsley et al. 1980, p. 11–26). In no instance was the significance of the conclusions altered.

To determine whether area or height of the fish aggregations had changed the result of acoustic trials, analyses of variance and covariance were performed using the response variable

$$(3) \quad y_{ij} = \ln \left[\frac{\left(\sum_{k=1}^3 \sum_{l=1}^2 X'_{ijkl} \right)}{6} \right]$$

where $y_{ij} = \ln$ – relative change in aggregation size for the j th trial ($j = 1, \dots, 20$) of the i th treatment ($i = 0, 1$), $X'_{ijkl} = N$ th duplicate measurement ($N = 1, 2$) of the k th replicate operational transect ($k = 1, \dots, 3$) for the j th trial ($j = 1, \dots,$

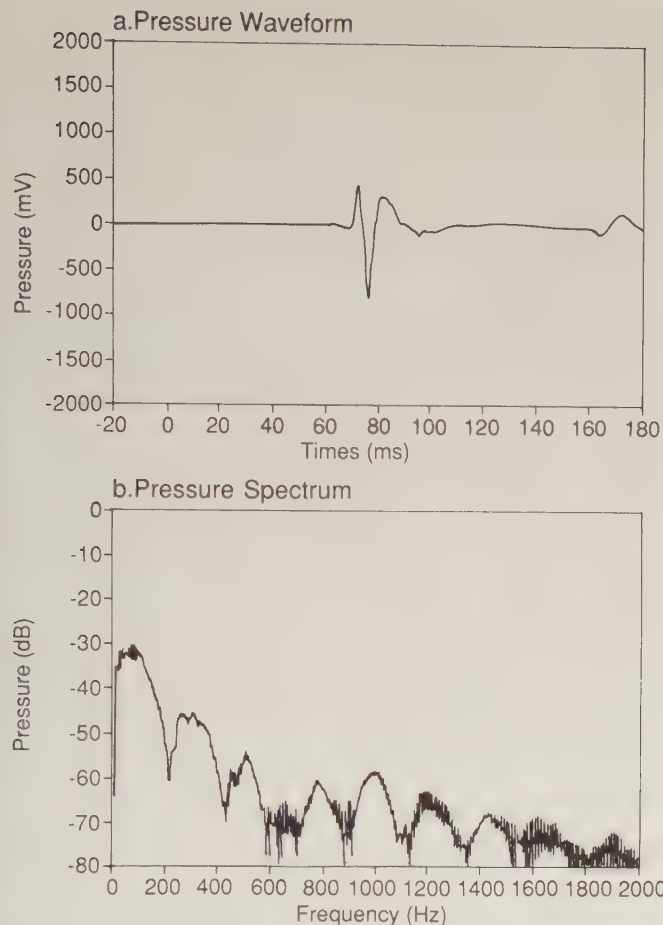


FIG. 2. Representative (a) air-gun signature and (b) pressure level spectrum measured by the spar buoy hydrophone at a depth of 60 m and at a range of 100 m. The single air gun used had a volume of 1639 cm³. Calibration: (a) 1 V = 5.6 kPa; (b) 0 dBV = 188 dB re 1 μ Pa; band width = 5 Hz.

20) of the i th treatment ($i = 0, 1$), and X_{ijkl} = the N th duplicate measurement ($N = 1, 2$) of the k th replicate preoperational transect ($k = 1, \dots, 3$) for the j th trial ($j = 1, \dots, 20$) of the i th treatment ($i = 0, 1$). Because rockfish aggregations have been reported by fishermen to either expand or contract in the presence of an acoustic disturbance, two-tailed tests of effects were performed. To interpret the nonrejection of a null hypothesis, post hoc power analysis was performed.

Results

Sound Characterization during the Fishing Experiment

Measurements showed that sound propagation from the air gun followed spherical spreading laws (Malme et al. 1986) and was not significantly changed by fluctuations in near-surface temperature structure during the trials. Pressure signature and pressure level spectrum that would be experienced by a fish aggregation at a depth of 60 m and at a range of 100 m from the sound source are shown in Fig. 2.

The bubble source used to simulate the surface effects of air-gun operation during mock or control emission was not impulsive but operated in 1-s bursts at a rate of six bursts per minute. The sound produced by its operation contained primarily high-frequency energy. The pressure signature and pressure level spectrum observed by the spar buoy hydrophone during the bubble source operation at a distance of about 80 m

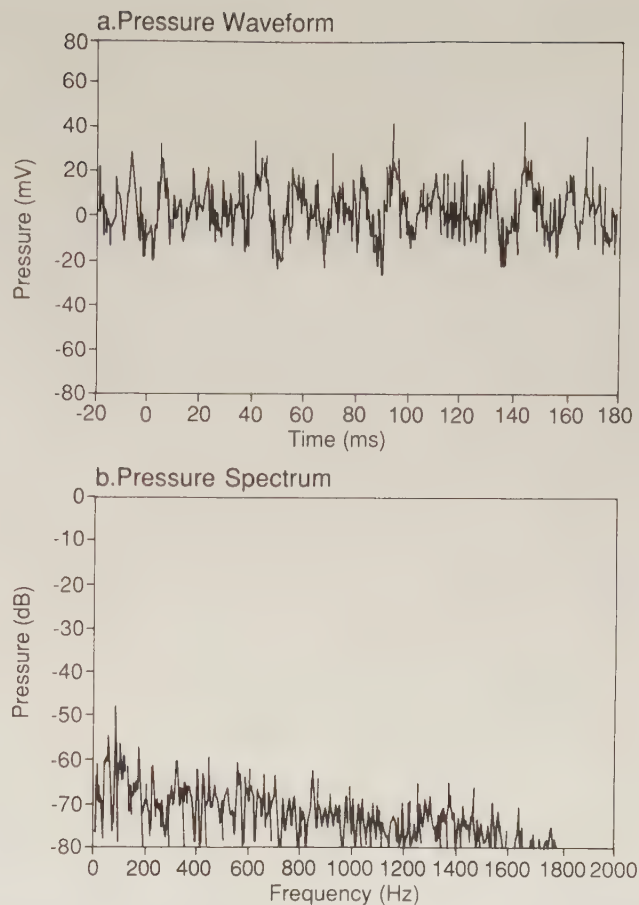


FIG. 3. (a) Acoustic signature and (b) pressure spectrum measured by the spar buoy during bubble source operation at close range (primarily dominated by radiated noise from the M/V NAUTILUS). Calibration: (a) 1 V = 178 Pa, (b) 0 dBV = 158 dB re 1 μ Pa; band width = 5 Hz.

are shown in Fig. 3. This record has been processed to retain sound energy at frequencies below 1.5 kHz to make it comparable with the air-gun records. Sounds recorded during bubble source operation were a combination of ambient noise and radiated noise from the M/V NAUTILUS. Because no change was observed in this frequency range whether or not the bubble source was operating, no acoustic influence on the fishing tests was expected from the pulsing of the bubble source.

Effects on Catch-per-Unit-Effort (CPUE)

The CPUE based on the catch of all species showed (Fig. 4) a significant curvilinear relationship as a function of trial depth ($r^2 = 0.534$) with the maximum predicted catch at approximately 146 m. Control trials had a mean depth of 124 m, and emission trials were conducted at a mean depth of 107 m. Analysis of covariance indicated a significant decline ($\alpha = 0.016$) in the mean total catch of rockfish per trial under emission conditions after adjustment to a common depth (Table 2). At a depth of approximately 109.7 m, control trials had a predicted mean catch of 34.0 (CI(23.5 $\leq \mu_C \leq$ 49.0) = 0.90) fish, while emission trials had a mean catch at the same depth of 16.2 fish (CI(11.0 $\leq \mu_E \leq$ 23.6) = 0.90). This difference represents an RC in mean catch of -52.4% (CI(-27.9% $\leq$ RC $\leq$ -76.9%) = 0.90) as a result of the acoustic emissions under the fishing conditions of this study.

To provide a second analysis of the catch that also takes into account differences in mean trial depth, only those trials con-

ducted at depths ≤ 118.9 m were analyzed. Eight control trials (mean depth 99.2 m) and 15 emission trials (mean depth 100.5 m) were conducted within that depth class. Covariance analysis indicated no significant relationship ($P(F_{1,20} > 0.1860) = 0.671$) between catch and depth within this subclass of trials. A subsequent two-sample t -test [$P(t_{21} \leq -2.0808) = 0.025$] nevertheless indicated a significant difference in mean catch between control and emission trials. For trials at ≤ 118.9 m, the relative change in catch was -47.0% as a result of acoustic emissions ($CI(-17.8\% \leq RC \leq -76.1\%) = 0.90$).

For the five most abundantly caught rockfish species, three species showed significant declines in catch associated with acoustic emissions after adjustment of the mean catches to a common depth (Table 2) (chilipepper, $P(t_{35} \leq -1.7341) = 0.046$; bocaccio $P(t_{37} \leq -2.6057) = 0.007$; and greenspotted rockfish, $P(t_{38} \leq 2.1109) = 0.021$).

The catch of chilipepper showed a cubic response with depth ($P(F_{3,35} > 35.9500) \approx 0$) and bocaccio a linear response ($P(F_{1,35} > 13.5627) = 0.00007$), while no relationship was found between the catch of greenspotted rockfish and trial depth ($P(F_{1,35} > 2.3030) = 0.138$). The decline in CPUE across species strengthens the conclusion that the observed differences are real and are not the result of chance.

Effects on the Cash Value of the Catch

A covariance analysis using a quadratic regression between the cash value of the catch and trial depth was performed (Fig. 5). The adjusted mean of the $\ln(\text{cash value} + 1)$ for emission trials was significantly lower ($P(t_{36} \leq -1.8503) = 0.036$) than the mean value for control trials (Table 2). After adjustment to a mean depth of 109.7 m, control trials had an average cash value of \$51.33 ($CI(34.27 \leq \mu_c \leq 76.62) = 0.90$), while emission trials yielded a mean cash value of \$25.78 ($CI(17.05 < \mu_e < 38.72) = 0.90$). This difference in economic return represents a relative change of -49.8% ($CI(-21.7\% \leq RC \leq -77.9\%) = 0.90$) in the dollar value of fish caught per trial under emission and fishing conditions of this study. This average decline in economic value of the catch takes into account all species caught. For both CPUE and cash value, the estimated declines do not take into account any alternate fishing strategies which might mitigate such losses.

Effects on the Rockfish Aggregations

Two possible covariants used in the analysis of aggregation area were the trial depth and the fraction of pelagic fish in the

aggregation as characterized by the catch composition (i.e. chilipepper, bocaccio, and greenstriped (*S. elongatus*), yellowtail, olive (*S. serranoides*), and widow (*S. entomelas*), rockfish) versus primarily demersal fish (i.e., cowcod (*S. levis*) and vermilion, greenspotted, yelloweye (*S. ruberrimus*), flag (*S. rubrivinctus*), canary (*S. pinniger*), starry (*S. constellatus*), rosy (*S. rosaceus*), copper (*S. caurinus*), greenblotched (*S. rosenblatti*), and rosethorn (*S. helvomaculatus*) rockfish). Bank rockfish (*S. rufus*) constituted only 1% of total number of rockfish caught and were not used in the analyses. Because pelagic species were found higher in the water column and were more mobile, it was suspected that this group of fish might respond differently to an acoustic disturbance. However, neither depth ($P(F_{1,37} > 0.6180) = 0.437$) nor fraction of fish which were pelagic ($P(F_{1,37} > 1.630) = 0.210$) was significantly correlated with the change in areal size of the aggregations (Equation 3) between preoperational and operational phases of the fishing trials. Further, the subsequent one-way analysis of variance indicated that no significant treatment effect was associated with any observed changes in the aggregation areal size ($P(F_{1,38} > 0.8084) = 0.374$) between phases of the fishing trials.

One of the more important observations obtained from the chart records is the fact that the aggregation area has tremendous temporal variation. The set of 20 control fishing trials exhibited substantial decreases, as well as large increases, in aggregation area size between preoperational and operational phases. The same observation pertains to emission trials. Under control and emission conditions, the response variable (Equation 3) for areal size had means of 0.1706 and 0.3127, respectively. In other words, an 83% change in the observed response occurred under emission conditions. However, with an error variance of 0.2496, the field study had a power of only $1 - \beta = 0.206$ of detecting a significant effect at $\alpha = 0.10$ with a change as large as the 83% shift observed. Indeed, as many as $n = 260$ replicate trials would be required per treatment to have a power of $1 - \beta = 0.90$ to detect the observed difference of 0.1421 ($= 0.3127 - 0.1706$, significant at $\alpha = 0.10$). Consequently, a few scattered observations lacking experimental control as in the report by Greene (1985) may result in conclusions which are misleading about the amplitude and direction of the response. This post hoc power analysis indicates that a shift in the areal size of aggregations is an extremely insensitive response variable for detecting the effects of air-gun sounds.

The mean change in aggregation height between trial phases (Equation 3) proved significantly different ($P(F_{1,37} > 2.9501)$

TABLE 2. Unadjusted and adjusted (to a common depth) means of $\ln(x + 1)$ based on covariance analysis of the total catch and catch of five rockfish species and cash value with corresponding 90% confidence intervals (CI) and tests of significance.

Response variable	Control			Emission			Test of adjusted means (α)
	Unadjusted mean	Adjusted mean	Adjusted mean 90% CI	Unadjusted mean	Adjusted mean	Adjusted mean 90% CI	
Total catch	3.8300	3.5554	$3.198 \leq \mu_c \leq 3.913$	2.5694	2.8440	$2.487 \leq \mu_e \leq 3.201$	0.016 ^a
Species catch							
Chilipepper	2.4812	1.8913	$1.509 \leq \mu_c \leq 2.273$	0.7125	1.3025	$0.921 \leq \mu_e \leq 3.201$	0.046 ^a
Vermilion rockfish	1.3015	1.0759	$0.662 \leq \mu_c \leq 1.490$	1.2059	1.4315	$1.018 \leq \mu_e \leq 1.846$	0.835
Bocaccio	1.4019	1.2736	$0.889 \leq \mu_c \leq 1.660$	1.2736	0.5467	$0.162 \leq \mu_e \leq 0.931$	0.007 ^a
Yellowtail rockfish	0.7432	0.9480	$0.512 \leq \mu_c \leq 1.384$	0.8890	0.6842	$0.248 \leq \mu_e \leq 1.120$	0.205
Greenspotted rockfish	1.0461	— ^b	$0.766 \leq \mu_c \leq 1.326$	0.5505	— ^b	$0.271 \leq \mu_e \leq 0.830$	0.029 ^a
Cash value	4.2328	3.9576	$3.563 \leq \mu_c \leq 4.352$	3.0122	3.2875	$2.893 \leq \mu_e \leq 3.682$	0.036 ^a

^aSignificant decline ($\alpha \leq 0.10$) attributed to acoustic emission.

^bUnadjusted means used because no significant relationship was found between catch and depth of trial ($\alpha = 0.138$).

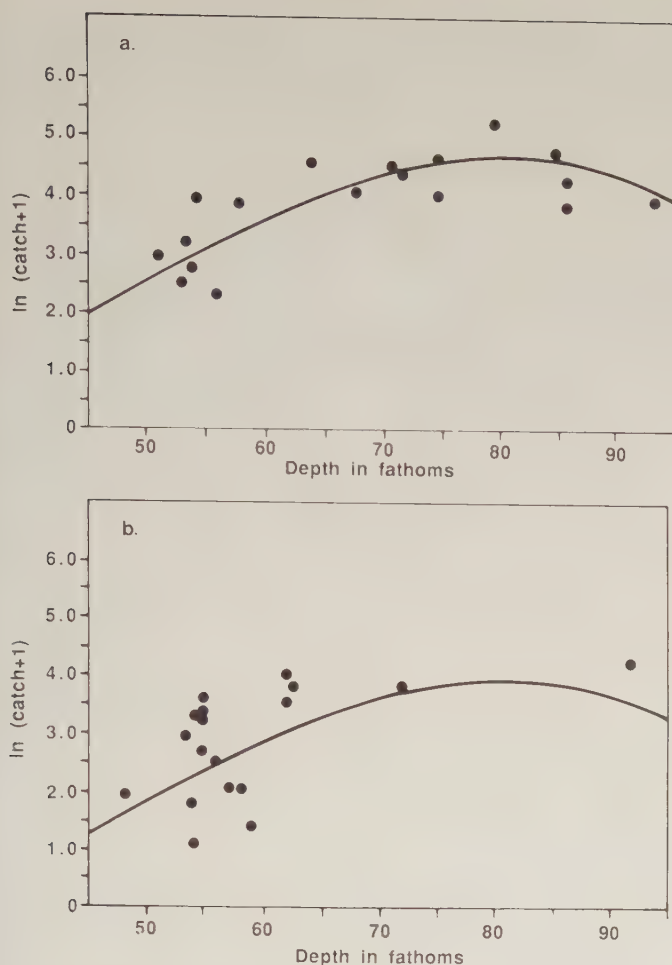


FIG. 4. Regression curves for $\ln(\text{catch} + 1)$ as a cubic function of the trial depth for (a) control and (b) emission trials. The multiple regression coefficient was $r^2 = 0.534$ for the fitted covariance model.

= 0.094) between control and emission trials after adjustment for species composition (i.e. portion of fish which were pelagic). Plots of the relative change in aggregation height (Fig. 6) indicated that under control conditions, there was a tendency for no change in height when the aggregations were composed entirely of demersal species. Alternatively, as the aggregations became more and more composed of pelagic species (e.g. chilipepper), the aggregation height increased by 24% between preoperational and operational phases of the setline fishing (right side of Fig. 6a). In other words, pelagic species like the chilipepper had a tendency to "flare" up the setline during fishing, while demersal species tended to be vertically stationary under control conditions (Fig. 6a). Under acoustic emission conditions (Fig. 6b), there was an across-the-board decrease in aggregation height regardless of species composition. As the species composition became entirely composed of demersal species, the height of the aggregations decreased by 26% between phases (left side of Fig. 6b). As the catch became entirely composed of pelagic species, aggregation height decreased by 8% between trial phases (right side of Fig. 6b). This phenomenon could have been masked had there not been rigorous use of control trials during the field experiment.

Discussion

In this study, the simple treatment design of a control and the worst-case scenario (within the limitations of a single air gun), in which the geophysical survey vessel traverses over the

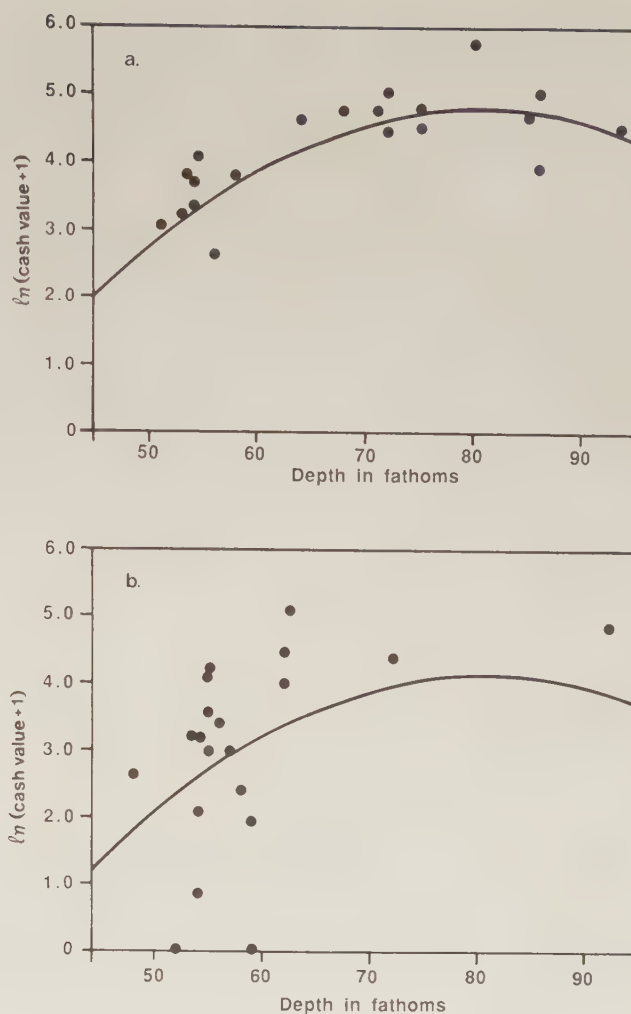


FIG. 5. Regression curves for $\ln(\text{cash value} + 1)$ as a quadratic function of the trial depth for (a) control and (b) emission trials. The multiple regression coefficient was $r^2 = 0.468$ for the fitted covariance model.

fish aggregation, was tested.) The purpose of this treatment design was to verify or refute allegations that sounds from an air gun affect fish catchability. The results substantiate an effect on CPUE under certain circumstances. Under emission conditions, the fishing experiment revealed a substantial ($RC = -52.4\%$) and statistically significant ($\alpha = 0.016$) decrease in the catch of rockfish. Significant declines in catch were also observed for three of the five most abundant rockfish species. Further, the results held regardless of whether all fishing trials or only those ≤ 118.9 m were analyzed. The observation of significant decline in several species as well as total catch strengthens the credibility of the findings.

The available evidence suggests that the reduced catchability derived from behavioral changes. Results of the behavioral experiment (Pearson et al. 1992) suggest changes in swimming behavior of rockfish from directed movement to milling or undirected movement (i.e. eddying behavior) at sound levels as low as 168 and 154 dB, respectively. Alarm behavior was exhibited during the behavioral experiment at sound exposure levels over the range of 178–207 dB, with a threshold for startle responses between 200 and 205 dB. Mean peak pressures of 186–191 dB at the base of the rockfish aggregations during fishing trials therefore appear to have been sufficient to elicit changes in swimming and schooling behavior but not sufficient to consistently elicit startle responses. In the fishing experi-

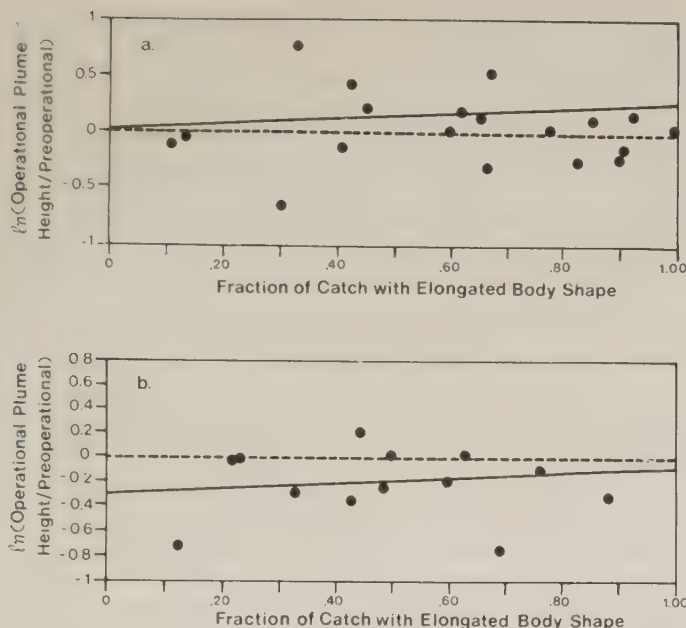


FIG. 6. Regression curves during (a) control and (b) emission trials for $\ln$ (operational phase height/preoperational phase height) as a linear function of the proportion of the catch composed of pelagic species (e.g. chilipepper). The multiple regression coefficient was $r^2 = 0.146$ for the fitted covariance model.

ment, height but not the areal size of the aggregations decreased under sound emission, suggesting that fish schools in the water column collapsed toward the bottom but did not disperse from the pinnacles to an observable degree. Had trials been conducted on fish aggregations located along shale banks (fish aggregations at pinnacles tend to be more stationary), dispersal as a response to acoustic emissions might have had a greater contribution to CPUE changes. Under the conditions of the fishing experiment, we suggest that the mechanism underlying the CPUE decline was not primarily dispersal but rather decreased responsiveness to baited hooks.

The length of time after sound exposure that CPUE effects persist is not known. The return of fish to preexposure behavioral patterns occurred within minutes after sound exposures ceased in the behavioral experiment (Pearson et al. 1992), suggesting the effects on fishing may be transitory, primarily occurring during the sound exposure itself. Persistent effects on CPUE would likely occur if the intensity or duration of sound exposure was great enough to elicit dispersal of the fish from the area. The extent or pattern of sound exposure that would elicit dispersal effects has to be determined in future investigations.

Extrapolation of the results of this study to geophysical surveys has some uncertainties because the exposure regime used in this study differs in several aspects from that likely during a typical survey with an air-gun array. Seismic survey vessels conduct operations along tracklines so that the sound level at any given location increases as the vessel approaches, peaks when the vessel is closest, and then decreases as the vessel moves away. This regime of increase, peak, and decrease in sound pressure is repeated as each trackline is performed, and the sound levels at approach, peak, and departure increase or decrease depending on whether the trackline is conducted closer or farther from the location of interest. The fact that the source level for arrays (240–250 dB; Malme et al. 1986) is substantially higher than that for the single air gun used here (223 dB) argues for a greater extent of effects from an array. Although

single air guns have the same abrupt signature in all directions, large arrays show the abrupt signature that presumably elicits startle responses (Pearson et al. 1987) only in certain directions from the array (directly ahead, directly behind, directly underneath, and on each side, directly perpendicular to the array center; Malme et al. 1986). The limitation of the abrupt signature in certain directions around the array argues for lesser or more intermittent effects from an array's more intense sounds.

Despite these uncertainties, calculation of the sphere of influence about a typical survey trackline with a larger array suggests that the exposure regime of such a trackline would be similar to that of this study. In this study, during the deployment of the first setline, the rockfish aggregation received sounds above 180 dB from 120 discharges (20 min $\times$ 6 discharges/min) within 20 min. Examination of the trends in catch among the setlines indicated that the majority of the observed effect occurred within the deployment of the first setline (Pearson et al. 1987). For a typical array of 65 550 cm³ with 32 guns and a source level of 255 dB, the sound exposure from a trackline passing directly over a point at a depth of 100 m can be calculated from the sonar equation $S = SL - 20 \log R$, where S = sound level at the point, SL = source level at 255 dB, R = range in metres, and $20 \log R$ is the transmission loss. For a single tracking passing directly overhead and assuming typical vessel speed 11 km/h) and array discharge rate (6 discharges/min), at 100-m depth, an aggregation would receive sounds from approximately 89 discharges with abrupt signatures and levels above 180 dB within a 15-min period. With the array directly overhead, maximum sound level would be 200 dB at 100-m depth, substantially above the maximum of 193 dB produced at the same depth by the single air gun used here. This analysis indicates that sound exposures from a single trackline are sufficiently similar to those of this study to expect changes in rockfish behavior and catchability. Both the fishing experiment discussed here and the behavioral experiment of Pearson et al. (1992) indicate that the decreased responsiveness would derive from the fish exhibiting alarm responses and other behavioral changes under sound exposure.

For surveys with multiple tracklines, sound exposure at a single rockfish aggregation will vary as a function of trackline spacing. For a reconnaissance survey with a trackline spacing of 1.85 km, two to four tracklines would produce sounds above 180 dB at a point 100 m deep. For surveys requiring detailed information on the geological structure, trackline spacing can be as close as 25 or 50 m. For 50-m trackline spacing, about 37 tracklines would contribute sounds above 180 dB to a pinnacle at 100-m depth. Because of the several hours taken to conduct a single trackline, these sounds would occur as 15-min exposures scattered over 4–5 d. The prospects for effects on rockfish catchability from detailed surveys with close tracklines warrant concern.

Acknowledgements

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Spatial Analysis of Bering Sea Groundfish Survey Data Using Generalized Additive Models

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Generalized additive models (GAM) are herein applied to trawl survey data in the eastern Bering Sea with an eye to (1) detecting trends in groundfish distributions and (2) improving abundance estimates by including the trend. GAM is a statistical method, analogous to regression, but without the assumptions of normality or linearity that relate a response variable (in this case, fish abundance) to location (latitude and longitude) and associated environmental variables (e.g. depth and bottom temperature). GAM provided reasonable (i.e. high r^2) fits to the spatial distribution of five flatfish species and was able to define a spatial "signature" for each species, namely their preferred depth and temperature range. GAM also gave lower average abundance and abundance variability estimates for these five flatfish species than the stratified sampling procedure previously employed.

Les auteurs ont appliqué des modèles additifs généralisés (MAG) à des données de relevés par chalutage dans le secteur est de la mer de Béring en vue d'identifier des tendances dans la répartition des espèces de poissons de fond et d'améliorer les estimations de l'abondance en y incluant ces tendances. La MAG est une méthode statistique semblable à la régression, sauf qu'elle ne suppose pas une normalité ou une linéarité des données. Elle met en relation une variable de réponse (dans ce cas-ci, l'abondance du poisson) et un endroit (latitude et longitude) assorti de ses variables environnementales (par ex., profondeur et température des eaux du fond). L'application de cette méthode statistique a donné un ajustement adéquat (c.-à.d. une valeur élevée de r^2) de la répartition spatiale de cinq espèces de poissons plats et une "signature" spatiale de chaque espèce, c'est-à-dire la gamme de profondeurs et de températures qu'elle préfère. Elle a aussi donné des estimations moyennes de l'abondance et de la variabilité de l'abondance des ces cinq espèces de poissons plats moins élevées que la méthode de sondage stratifié utilisée auparavant.

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Annual groundfish surveys have been conducted in the eastern Bering Sea by the National Marine Fisheries Service (NMFS) Northwest and Alaska Fisheries Center (NWAF) continuously since 1979. These data have been used primarily to provide abundance estimates of the commercial fish species as an aid to setting fishing quotas. They also provide an opportunity to examine the spatial distributions of these species and how they might be related to environmental factors (such as depth and bottom temperature) and biological factors (such as the presence or absence of other species or the distance from a spawning area). Also, the existence of trends in spatial distribution may bias the estimates of average abundance and (especially) its variance and detection and estimation of these trends. Correction for these trends can lead to improved abundance estimates. Here we review the application of generalized additive models (GAM; Hastie and Tibshirani 1986; 1990; Kaluzny 1987) for detecting significant trends in the spatial distribution of several flatfish species on the eastern Bering Sea shelf and relate these trends to two potentially important covariates: depth and bottom temperature.

Flatfish have been chosen for this study from among the fish surveyed because (1) they appear to have a high degree of species-specific fidelity in their spatial distribution from year to year, (2) each species has a spatial "signature" that we hope

can be characterized in relation to "controlling" covariates, and (3) they are denizens of the bottom stratum of the shelf and are therefore the most completely available to the trawl gear used of all the fish species (i.e. there is little problem with incomplete catchability or with size-catchability interactions).

Spatial Statistics and the GAM

Spatial statistics concern the analysis of data having an explicit spatial component. This criterion is eminently satisfied by fisheries survey data in that each sample is located explicitly in space by latitude and longitude. Besides being georeferenced, these data are also multivariate in that counts and biomass estimates are made at each sampling location for each species group sampled. The data can be categorized as multivariate point data in that the locations of the data collection points can be indicated on a map, but that more than just the sampling point is important in specifying the data (unlike some data in which the locations themselves are the primary variable of interest, a so-called spatial point process). While the statistical analysis of point processes concerns the distribution of distances between points or the numbers of points in bins of given sizes, the statistical analysis of multivariate point data emphasizes either the spatial correlation (aggregation) or trend

in the variables of interest. Spatial correlation, the correlation between variables in space as a function of the distance between them, generally is assumed to follow some underlying function. This is used, for example, in kriging, where spatial autocorrelation is assumed to be an explicit function of the distance between the sample points. This function is called the semi-variogram (Journel and Huijbregts 1978). Generally, the semi-variogram is assumed to be space and direction nonspecific (called stationarity and isotropy, respectively). Usually meeting this assumption requires some transformation of the data (Sullivan 1991). Given the semi-variogram, the kriging algorithm is used to estimate the value of the variable of interest at points other than the sampled points, thereby providing a map for the variables over the region of interest.

In cases where the average value of a variable changes explicitly over space, this change is assumed to be a trend. By a *spatial trend*, we mean a change in the average response variable (density) which is a function of the spatial location. It is the detection of, testing for, and implications of trends in abundance that we are concerned with in this paper. There is no reason to believe that a survey which covers a large area and is based on a grid size of tens of kilometres (37×37 km in the case of the Bering Sea groundfish survey) could give any information on the aggregation, spatial correlation, or patchiness of the species and so we ascribe such changes in this case to spatial trends. Besides detecting trends in abundance over space, we are also interested in relating these changes quantitatively not only to spatial location but to environmental factors such as depth and temperature. The existence of such quantitative relationships strengthens our understanding of the factors that influence the explicit spatial distribution of fish species abundance and also gives us a degree of explanation of this distribution that may serve to reduce the variance in abundance estimates by providing additional information about abundance distribution through covariates that are easy to measure.

The mainstream solution to abundance estimation problems caused by the spatial distribution of animals is to stratify the data, and possibly also the sampling scheme (Hsu 1987). However, this stratification has to be based on some criteria external to the data (e.g. location) and not on the actual observations. Poststratification of the data based on the observed densities may result in a considerable downward bias in the variance estimates. A stratification of the sampling program could overcome some of the problems, but detailed species-specific stratification is not feasible for general surveys, which collect information on several species simultaneously.

In order to model the spatial distribution of surveyed animals, we will use GAM (Hastie and Tibshirani 1986, 1990). More specifically, we use GAM in which we assume that the numbers of animals are distributed according to a nonhomogeneous Poisson process with the intensity being a function of spatial location (or some spatially related covariates).

GAM allows us to relate the changes in abundance to spatial covariates, without restricting the functional form of the relationship (Kaluzny 1987; Hastie and Tibshirani 1990). This method allows us to have nonlinear trends and to include covariates which potentially determine the spatial patterns in the data. Bootstrap methods give information on the variability around the trends, and permutation or randomization tests (Box et al. 1978) are used to determine the significance of trends. The use of GAM for analyzing survey data is quite general in that the surface which is fitted to the data is only restricted to be a sum of smooth nonparametric functions. The form of the functions is not restricted to polynomials as in generalized lin-

ear models (GLM; Nelder and Wedderburn 1972; McCullagh and Nelder 1989). The functions are instead determined by a smoothing technique that reflects local spatial trends, while allowing trends over the entire space to be observed (if they exist).

GAM is a nonparametric generalization of multiple linear regression. Both methods relate the dependent variable to possibly important covariates. However, in GAM, the covariates are assumed to affect the dependent variable through additive, unspecified (not linear) functions. Scatterplot smooths (Chambers et al. 1983) in GAM replace least square fits in regression. In GAM, the data can come from any distribution in the exponential family (which includes the normal, Poisson, and binomial distributions). In our application, the data were assumed to come from a Poisson distribution. This distribution was chosen because it is often appropriate for counts data (in this case, we are looking at estimates of fish abundance in terms of fish numbers) and because the Poisson distribution is generally used in spatial data analysis as a null hypothesis instead of the normal distribution (Diggle 1983). The following discussion of GAM assumes an underlying Poisson distribution.

GAM for Spatial Data

In an additive model, the expected value of a random variable Y is expressed as a sum of smooth functions of the covariates. Thus,

$$(1) \quad E(Y|x_1, \dots, x_p) = \sum_{j=1}^p S_j(x_j)$$

where $S_j(x_j)$ represent smooth functions of the p covariates. In a GAM, a known function of the expected value, called the link function, is modeled as a sum of smooth functions of the covariates. This generalization of the model is easy to make for random variables in the exponential family.

A central assumption in the GAM for spatial data is that the observations are distributed according to a nonhomogeneous Poisson distribution. The parameter of the Poisson distribution

is $\Lambda(x) = \int_{A_x} \lambda(u) du$ where $\lambda(x)$ is the intensity of the under-

lying Poisson process and A_x is the area of the observations. The expected value of the Poisson distribution is $\Lambda(x)$ and the natural link function is the logarithm. Thus, the Poisson generalized additive model relates the expected counts to the covariates as

$$(2) \quad \log \left[E(Y|x_1, \dots, x_p) \right] = \log \left[\Lambda(x) \right] = \sum_{j=1}^p S_j(x_j).$$

Or, if the additive predictor is $\eta = \sum_{j=1}^p S_j(x_j)$, then

$$\Lambda = \mu = e^\eta.$$

Since the functional form of the smooth functions $S_j(x_j)$, $j = 1, \dots, p$, is not specified, the usual estimation techniques such as maximum likelihood estimation cannot be used for GAM. Instead, an algorithm that empirically maximizes the expected log-likelihood is used. The derivative of the expected log-likelihood is set to zero and the resulting equation is expanded in a Taylor series about an initial estimate of the additive predictor, η° . The equation can then be rearranged to give a new estimate for η based on the initial estimate η° . This update equation is used iteratively with the conditional expectation from the expected log-likelihood estimated by a scatterplot

smoother. The resulting algorithm is similar to the adjusted dependent variable regression method of Nelder and Wedderburn (1979) for computing maximum likelihood estimates when the predictor, η , is a linear function of the covariates. The adjusted dependent variable for the Poisson generalized additive model at the m th iteration is

$$(3) \quad z^m = \eta^m + \frac{(y - e^{\eta^m})}{e^{\eta^m}}.$$

The scatterplot smooth of z^m on x (when there is only a single covariate x) provides an updated estimate of the additive predictor, η^{m+1} .

The measure of fit for the generalized additive models is the deviance, which is twice the log of the likelihood ratio between the saturated model and the current model. For the Poisson model, this is calculated as

$$(4) \quad \text{Dev}(y, \mu) = 2 \sum_{i=1}^n \left[y_i \log \left[\frac{y_i}{\mu_i} \right] - (y_i - \mu_i) \right].$$

The updating iterations are continued until the deviance fails to change.

Backfitting algorithm

The above discussion of the Poisson generalized additive model was for only one covariate, x . For the spatial models that will be considered, there will be at least two covariates, e.g. longitude and latitude. To fit multiple covariates, the backfitting algorithm is used. The algorithm computes the smooth function for each of covariates by holding the other covariate functions fixed. To do this for the j th covariate, x_j , the partial residual

$$(5) \quad r_j = z - S_0 - \sum_{k \neq j} S_k(x_k),$$

where z is the adjusted dependent variable described in Eq. (3), is formed. An updated value of S_j is computed by smoothing r_j on x_j . The process is then repeated for each covariate.

The initial estimates for the algorithm are zero for the smooth functions S_j and the log of the overall mean count for η . The algorithm is iterated until the deviance no longer decreases or for a maximum set number of iterations.

Running line smoothers

The core of the GAM used in this paper is a running line smoother which is used to find the smooth functions S_j of Eq. (2). A running line smoother fits a line by least squares to the data points in a symmetric nearest neighborhood containing n_i points around each x_i . The advantage of a running line smoother over a running mean smoother is that it reduces bias near the endpoints without sacrificing much in calculation speed (Kaluzny 1987; Friedman 1984).

The span of the smoother (the fraction of the data set used in estimating a line at each point) is determined using cross-validation (i.e. the smooth value for the point x_i is computed by omitting the i th observation and the span is chosen so that the residual sum of squares is minimized). In the program used in this study, the best span was found by trying the spans 0.3, 0.4, 0.5, 0.6, 0.7, and 1.0 and choosing the one which gave the smallest residual sum of squares. A span of 1.0 uses all the data to fit the least squares line and is equivalent to a simple linear regression line.

Estimation of variability

In moving from the parametric generalized linear models fit by maximum likelihood to the nonparametric generalized addi-

tive models, the likelihood theory for estimating variances is lost. However, the bootstrap methodology of Efron (1982) can be applied to the additive models to obtain estimates of variability.

A bootstrap sample of size n is drawn from the observations (x_{1j}, x_{2j}, y_j) with replacement. The Poisson generalized additive model is fit to this sample and the resulting smooth functions S_1^* and S_2^* are saved. This is repeated N times. The spans for the running line smoothers used in the bootstrap fitting are fixed at the values chosen by cross-validation on the original data. If the span is allowed to vary for each bootstrap sample, a new model would be fit when we are interested in the variability of the model fit to the original data. The upper and lower $\alpha/2$ empirical quantiles of the S_i^* at each x_{ij} gives an approximate $(1 - \alpha) \times 100\%$ prediction interval for S_i at that value of x_i .

Test of trend significance

The bootstrap prediction intervals are one method to assess the significance of the smooth functions. The intervals indicate a range of possible values the function could have. If a horizontal line can be drawn within the prediction interval, then there is an indication that the smooth function is not significant. A more formal approach is to do a permutation test. The null hypothesis that is considered by the test is

$$H_0: S_i(x_{ij}) = m \text{ (a constant) for all } j,$$

i.e. the smooth function for covariate x_i does not depend on x_i . Under this null hypothesis, any permutation of $(x_{i1}, x_{i2}, \dots, x_{in})$ should result in approximately the same overall fit. If the null hypothesis is false, then permuting the values of x_i should not result in as good a fit as that obtained from the original data. Here, by "good fit" we mean small deviance. To provide a familiar measure of model fit, we compute a pseudocoefficient of determination R^2 as the fraction of the total deviance explained by the model (1.0 minus the ratio of the deviance in the best fitting model to the deviance for the model with just the overall mean, the null or zero model). While not identical to the classical R^2 , this measure is bounded between 0 and 1 and is used as a surrogate for R^2 . Since we cannot examine all possible permutations, we only use a sample of size N of the possible permutations. We record the deviance from the generalized additive fit to each of the N permutations of the covariate vector x_i along with the other unpermuted covariates. To avoid changing the model being fit, the same fixed span smoother is used for all the fits, with the span being chosen by cross-validation on the original data. If the deviance from the original data is the m th smallest among the $N+1$ deviances, the null hypothesis is rejected at the $m/(N+1)$ level.

Survey Data

The groundfish surveys used as data for this study have been collected annually since 1979 in the eastern Bering Sea between latitudes 54 and 63°N and from longitude 180°W eastward to the Alaska coast (Fig. 1). Samples were taken over a regular grid at 37-km intervals (closer together at some locations) using bottom trawl gear. Sampling was done from June to August. Tows were made for a 30-min period at a towing speed of 6.3 km/h (Smith and Bakkala 1982). Fish were sorted and lengths and weights determined for subsamples (for hauls larger than 1150 kg). Average bottom depth and gear temperatures were measured for each tow. Because the hauls can be expressed in terms of numbers of fish, the Poisson distribution was chosen for the underlying abundance distribution. Sampling proceeded from east to west beginning in Bristol Bay in

Haul Stations 86

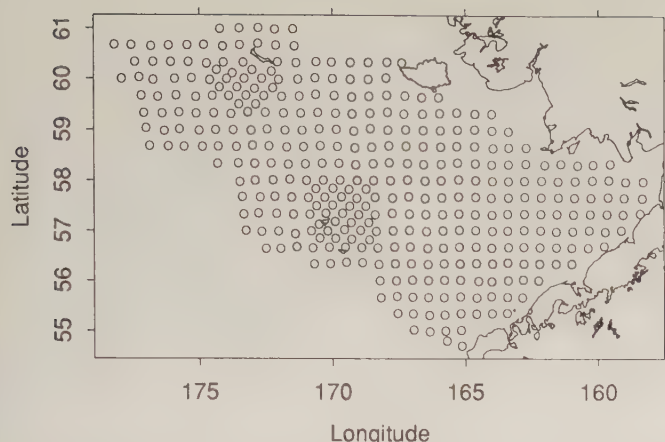


FIG. 1. Haul stations visited by NMFS Service eastern Bering Sea groundfish survey from 1979 through 1987.

June to intercept migrating species in the same way each year. The five study species selected for this report are yellowfin sole (*Pleuronectes asper*, previously *Limanda aspera*), Greenland halibut (turbot) (*Reinhardtius hippoglossoides*), rock sole (*Pleuronectes bilineatus*, previously *Lepidopsetta bilineata*), flathead sole (*Hippoglossoides elassodon*; also included Bering flounder, *Hippoglossoides robustus*), and Alaska plaice (*Pleuronectes quadrituberculatus*). The same area was surveyed from year to year, although some changes were made in fishing gear, which makes comparisons between years less reliable than within-year comparisons. Representative spatial distributions for each species for 1986 are shown along with depth contours in Fig. 2. Initial perusal of these data, and those for all years, suggested that each of the species has a different spatial distribution and these distributions are fairly consistent from year to year. Furthermore the distributions appear to be related to depth.

GAM Data Analysis

Two GAMs were done for each fish species and year (Table 1). Model 1 represents the average abundance as related to bottom depth and temperature. Model 2 additionally adds latitude and longitude as covariates. For the latter GAM, the latitude–longitude axes are rotated to maximize pseudo- R^2 . Table 1 displays the pseudo- R^2 for each of the GAM runs, and also gives the rotation angle giving the highest pseudo- R^2 for model 2.

The difference in pseudo- R^2 between models 1 and 2 gives an indication of how well depth and temperature alone explain the distribution. Having a modest increase in pseudo- R^2 , as for yellowfin sole in most years, suggests that little additional information is provided by including latitude and longitude. In these cases, where pseudo- R^2 is greater than 50%, depth or temperature (or both) appears to affect the spatial distribution of abundance. For cases where the pseudo- R^2 for model 2 is high but for model 1 is low, as with Alaska plaice for several years, some other factor besides depth and temperature, related to location, appears to affect the distribution. In cases where the pseudo- R^2 is low for both models (e.g. flathead sole and Bering flounder in 1982), it may be that the spatial distribution is not coherent enough to accept the GAM fit as significant.

Figure 3 displays results of the GAM fit compared with the raw data for rock sole in 1985, in a variety of formats. It serves

to display some of the strengths and weaknesses of GAM. Because it is based on a smoothing algorithm, GAM clearly smooths out the peaks and troughs of the raw data. Examining the spatial distribution of the residuals in Fig. 4, it is apparent that the residuals are not randomly distributed in space, but instead there are clusters of + and - residuals. Perhaps this reflects spatial autocorrelation between neighboring survey sites, or some more local (but still spatially extensive; remember the survey sites are separated by 37 km) phenomenon that we are not aware of. If the clumping of residuals is due to spatial autocorrelation, kriging (Cressie 1985), which explicitly includes this factor, can be used to improve the model fit to the abundance data.

Significance Tests of GAM Fits

As mentioned earlier, a permutation test was used to test the significance of depth and temperature as covariates for abundance. This involved 500 runs apiece of the GAM algorithm with either the depth or temperature values permuted between the locations. The α level for the test is the order of the pseudo- R^2 for the GAM applied to the original data compared with the R^2 for the 499 other GAM runs with permuted depths or temperatures. The rationale is that if the fit is significant, then it should give a higher pseudo- R^2 than most of the fits in the other permutations, which had the covariate of interest scrambled randomly between sites.

Results of this test (Table 2) show that depth is statistically significant at the 0.002 level for all depth runs, and for most temperature runs at a level less than 0.1. There are exceptions for the temperature test, especially yellowfin sole in 1982. As might be surmised from the number of runs, this test is computationally intensive. Because depth and temperature are strongly correlated with each other and because depth is consistently a more significant effect, we suggest that depth is the primary determining factor for abundance of Bering Sea flatfish (but see the discussion section for possible exceptions).

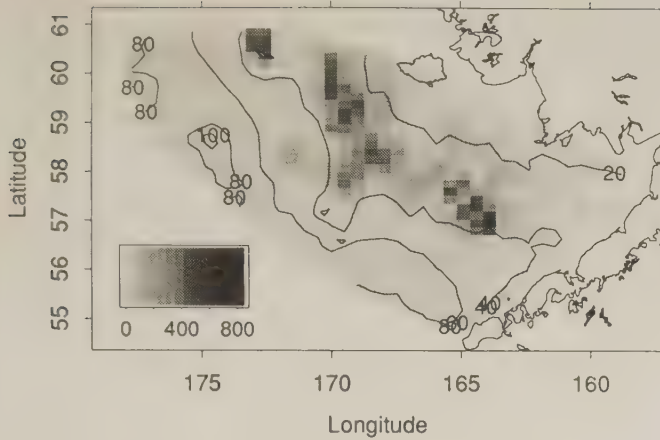
Model Variance Estimates

Model variance estimates for the smooths are generated using bootstrap resampling of the original data (Efron 1982). The GAM algorithm is rerun for each resampling; in our case, we used 400 resamples. The sampling was done with replacement, and interpolations were used to fill in at locations where no sample points were taken. This variance estimation method is extremely computationally intensive and requires the display of the output of 400 GAM fits. Figure 5 shows plots of the best fitting GAM smooths for depth (metres) and gear temperature (bottom temperature, degrees Celsius), along with 90% confidence limits from the bootstrap resamples, for selected fish species in 1986. These plots are useful for displaying the form of the relationship between the logarithm of abundance and covariates that are hypothesized to be important in affecting abundance. They also provide a measure of the tightness of the fit. In fact, plots of the smooths along with bootstrap-generated 90% confidence intervals can be used to provide another measure of significance of a covariance in addition (or as an alternative) to the permutation tests. A rule of thumb for significance is that a covariate is insignificant if a horizontal line can be drawn between the 90% confidence limits.

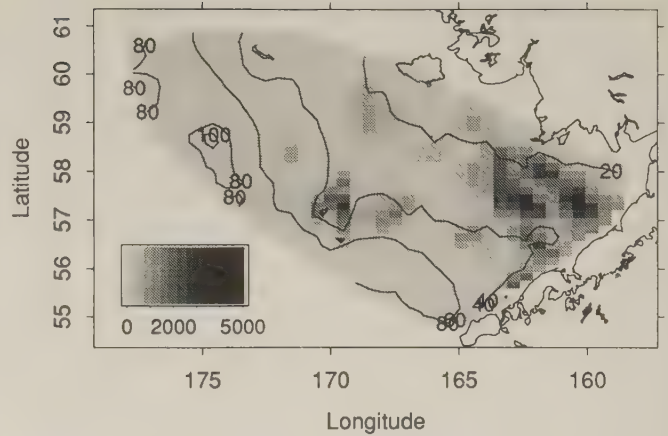
Spatiotemporal Effects: Multiyear GAM Runs

To test whether the “signature” for the flatfish species are truly the same from year to year, we conducted GAM analysis

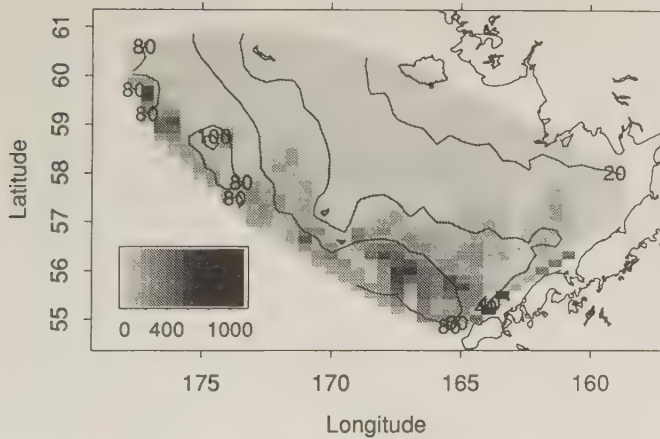
Alaska Plaice 86



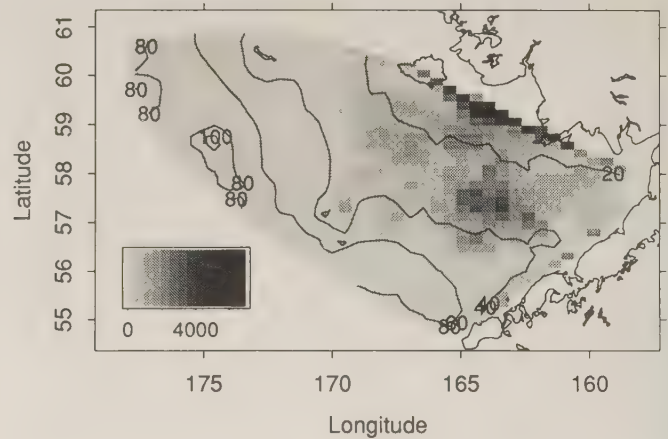
Rock Sole 86



Flathead Sole 86



Yellowfin Sole 86



Greenland Turbot 86

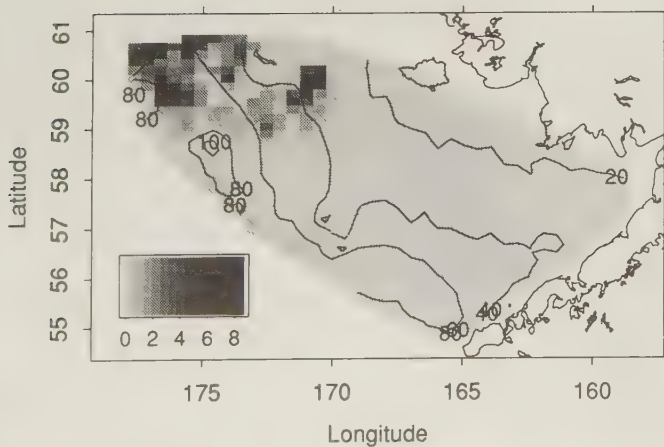


FIG. 2. Grey scale plots showing the spatial distribution of five flatfish species for the 1986 survey superimposed on a map of the eastern Bering Sea with 20-m isobaths.

on each species over the entire 1979–87 period, with covariates for depth, temperatures and year. The inclusion of a year effect allowed us to lump all years into the same analysis and to compare the GAM results for individual years with this combined analysis. Bootstrap resamples (400) were conducted for these

runs to provide error bounds on the smooths and are shown in Fig. 6. Pseudo- R^2 values for the pooled GAM runs were within the range of those for individual year runs (pseudo- $R^2 = 0.59, 0.48, 0.54, 0.41,$ and 0.42 for Greenland turbot, rock sole, yellowfin sole, Alaska plaice, flathead sole, and Bering floun-

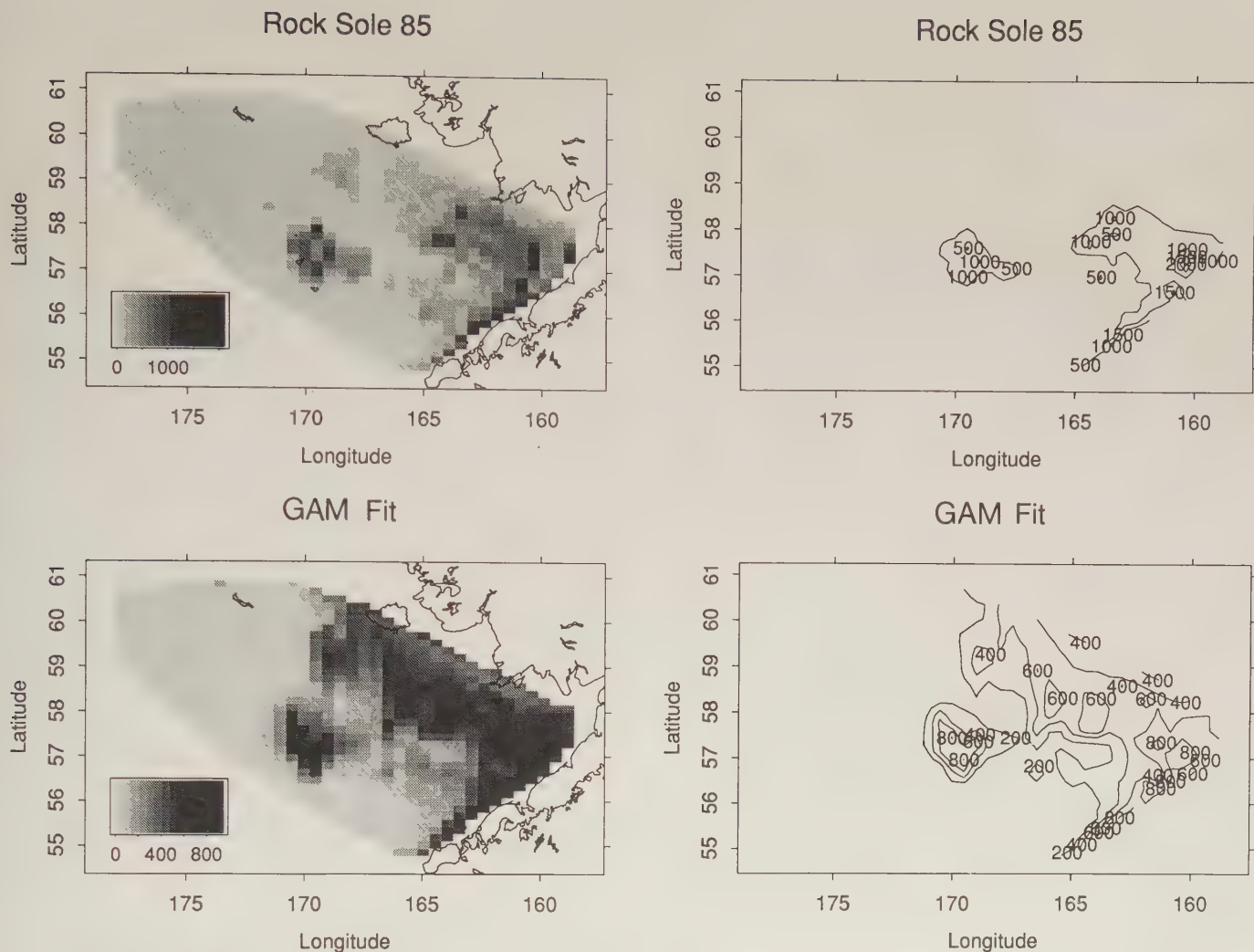


FIG. 3. Results of the generalized additive model fit compared with the raw data for rock sole in 1985. Results are shown as grey scale plot, contour plots, and three-dimensional plots. (Fig. 3 concluded next page)

TABLE 1. R^2 values of GAM for each species and year. Model 1: bottom depth and gear temperature; model 2: bottom depth, gear temperature, longitude, and latitude. Angle refers to clockwise rotation of the longitudinal axis.

		Year								
Species		1979	1980	1981	1982	1983	1984	1985	1986	1987
Alaska plaice	Model 1	33	52	61	34	51	48 ^a	48	60	42
	Model 2	64	75	74	70	62	59	66	67	54
	Angle	75	77	64	71	75	70	79	82	78
Flathead sole	Model 1	33	41	21	29	38	49	51	55	52
	Model 2	54	55	53	46	50	58	65	65	61
	Angle	86	90	65	59	81	82	0	82	75
Greenland turbot	Model 1	43	71	79	49	71	73	62	57	76
	Model 2	73	87	90	75	79	88	65	63	78
	Angle	71	66	68	57	67	71	9	81	43
Rock sole	Model 1	35	50	68	42	62	53	72	58	62
	Model 2	70	80	79	79	78	70	78	70	75
	Angle	55	70	11	73	3	60	74	9	59
Yellowfin sole	Model 1	56	68	68	58	62	62	— ^b	69	56
	Model 2	66	77	85	75	74	74	80	81	71
	Angle	14	87	0	7	1	39	38	86	83

^aConvergence not obtained in 100 iterations.

^bGAM gave anomalous results for this case.

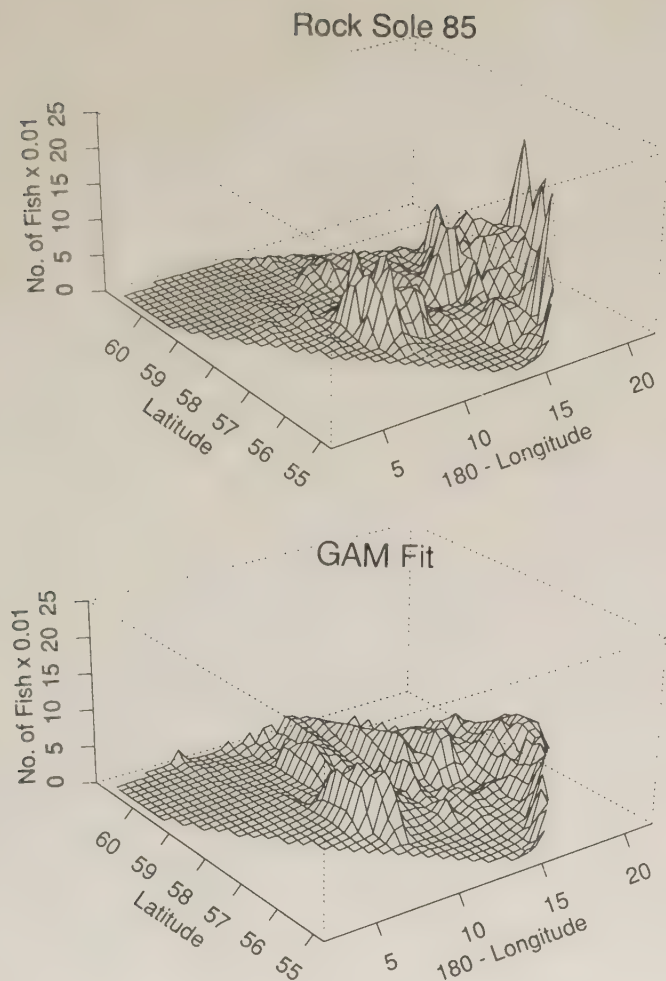


FIG. 3. (Concluded)

Residuals

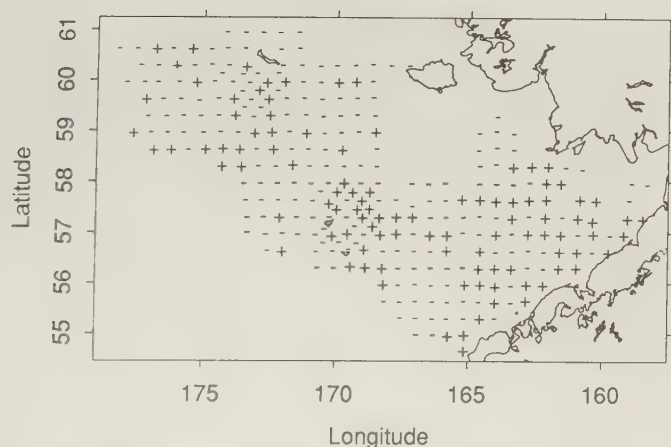


FIG. 4. Spatial distribution of residuals (denoted by + or -) of the GAM fit to the 1985 rock sole data. These show whether the residuals to the GAM fit are spatially randomly distributed.

der, respectively). This suggests that the spatial distributions for each species do not change markedly from year to year and, for the most part, are subject to the same environmental influences each year. This is further corroborated by the similarity

between the individual year GAM smooths on depth and those for the multiyear GAM fits (compare Fig. 5 and 6).

Abundance Estimation

One of the benefits of using GAM is that it provides a method for improving abundance estimates by using spatial trend information. We used generalized additive models combined with bootstrap sampling to generate estimates of mean abundance at each sampling point for each of the flatfish species. To allow comparison with abundance estimates made from the data by the NMFS, we used the same stratified estimation technique to estimate overall abundance for each species. For each species-year, 400 bootstrap samples of the raw data were generated. A GAM was fit for each bootstrap and a mean abundance estimate was obtained at each survey point sampled by the bootstrap, with the log-transformed estimates transformed back into direct abundance. A polynomial interpolation-extrapolation program was used on the GAM smooths to estimate abundance at points not sampled by that particular bootstrap (Press et al. 1989). GAM-estimated abundance at each survey location was converted to catch-per-unit-effort (CPUE) standardized to the performance of the vessel used for that year. Catch was the number of fish caught and effort the distance fished in kilometres. Following the NMFS procedure, the estimates were based on stratifying the sampling locations. First, the CPUE was estimated for each stratum:

$$\overline{\text{CPUE}_i} = \frac{1}{n_i} \sum_j^{n_i} \text{CPUE}_{ij}$$

where n_i is the number of stations in the i th stratum. In the NMFS procedure, the variance in CPUE for each stratum was estimated by

$$\text{Var}(\overline{\text{CPUE}_i}) = \frac{1}{n_i(n_i - 1)} \left\{ \sum_j^{n_i} \text{CPUE}_{ij}^2 - n_i \overline{\text{CPUE}_i}^2 \right\}.$$

The fish abundance in the i th stratum was estimated by NMFS as the ratio of the stratum area to the area covered by 1-km of towing, multiplied by the average CPUE for the stratum, while the variance was the square of this ratio multiplied by CPUE variance. Overall abundance was tallied as the sum of stratum abundances, while its variance was the sum of the variances assuming independence of variance between the strata. We preferred a variance estimate that did not assume variance independence between strata. The bootstrap resampling allowed such an estimate by computing independent mean estimates (by summing strata mean estimates) for each bootstrap resample and computing the variance of this mean from the independent bootstrap-based mean estimates. By this procedure, the strata were used solely as area weightings for the GAM-derived abundance estimates. Therefore, we could use the NMFS calculations of stratum area, rather than having to estimate the area of each sampling station by a method such as tessellation or polygon surface covering, without assuming independence between the strata.

Figure 7 gives the results of the GAM estimates for overall abundance for each of the five flatfish species for every survey year compared with the NMFS estimates, with a measure of variability given by deviation lines around the best estimates. For the NMFS estimate, we show the estimated mean abundance, while for the GAM estimate, we used the median of the 400 bootstrap estimates for each year. The median was used for the GAM estimates because it is more robust than the mean

TABLE 2. *P* values for permutation tests of the significance of depth and temperature as predictors of abundance in GAM. The number of permutations sampled (*N*) was 500.

Species	Predictor	Year								
		1979	1980	1981	1982	1983	1984	1985	1986	1987
Alaska plaice	Depth	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	Temp.	0.112	0.100	0.002	0.236	0.002	0.006	0.004	0.002	0.002
Flathead sole	Depth	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	Temp.	0.018	0.002	0.010	0.008	0.002	0.002	0.002	0.002	0.002
Greenland turbot	Depth	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	Temp.	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
Rock sole	Depth	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	Temp.	0.002	0.002	0.002	0.004	0.002	0.002	0.002	0.002	0.002
Yellowfin sole	Depth	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	Temp.	0.002	0.002	0.002	0.886	0.002	0.002	0.002	0.002	0.002

to outliers. Outliers in the data caused convergence problems in one of the bootstrap runs where an outlier was included in the bootstrap sample. The measure of variability is two standard deviations for the NMFS estimate and twice the median of absolute deviations (MAD) for the GAM estimate. A normalized measure of variability is given in Table 3. For the NMFS estimate, this is the coefficient of variation (standard deviation over mean), while for the GAM estimate, we used the MAD over the median. The MAD was multiplied by a correction factor (1.483) to make it consistent with the standard deviation of the assumed normal distribution in the NMFS model (our assumption was of an underlying Poisson distribution).

The GAM abundance estimates are consistently between 30 and 50% smaller than the NMFS estimates, and the normalized variation measure is also usually smaller. Which estimate is to be believed? There are two features of the GAM estimate that make both the GAM-derived expected value and variance lower than the NMFS estimate. First, the smooth of the GAM tends to reduce the effect of extremely large counts at individual stations. As such, the GAM estimate is more like such robust estimators as the trimmed mean, which downplay the effect of outliers or individual points strongly influencing the estimate. Second, the GAM estimate includes the effect of trends in abundance due to model covariates (especially depth). To the extent that these covariates exert a controlling influence on abundance this estimate will be an improvement over the NMFS estimate. The midrange values of most pseudo- R^2 in the GAM fits leave this second factor unresolved (Table 1). We do not think that the lower abundance estimates under GAM are due to the logarithmic transformation used. This is because (1) the values were transformed back to true abundance before CPUE and overall abundance were computed and (2) the logarithmic transformation is the required model transformation under the Poisson assumption. The bias introduced into *normally* distributed estimates under the logarithmic transformation when the data are transformed back does not extend to the Poisson distribution. One factor influencing the reduction in variance is our not assuming independence between strata in computing our variance estimate. Bootstrap resampling of the data allows a variance estimate for overall abundance independent from the strata. Actually, bootstrap resampling of the raw data could be done without GAM, and we recommend that it be used for future variance estimation for surveys involving stratification.

Discussion

Although some of the flatfish species are associated with each other (e.g. Bakkala 1980 reports data from a variety of sources

showing that yellowfin sole is most regularly associated with Alaska plaice), examination of the data (Fig. 2) suggests that each species has a distinct spatial distribution. Greenland turbot appears to be associated with depths greater than 40 m. This species is thought to spawn in the winter in the region between Unimak Pass and the Pribilof Islands (Alton et al. 1988). Greenland turbot larvae settle out in the northern and central Bering Sea continental shelf and the fish then move toward the continental slope as they age. Examination of the size distribution of the survey data (not yet done) should reveal a change in distribution with increased size toward increased depth. The eastern Bering Sea population of Greenland turbot represents only a small part of this species range, which is circumpolar, and even of the Bering Sea stock, most of which is in water deeper than that in the survey area. Changes in the annual abundance estimated from both GAM and NMFS methods (Fig. 7) indicate that the population of Greenland turbot has declined consistently over the study period, at least within the eastern Bering Sea Shelf.

Rock sole appears to be distributed widely along the Unalaska peninsula in southern Bristol Bay, with a second population in the neighborhood of the Pribilof Islands (Fig. 2). Although depth and temperature both significantly influence their distribution, rock sole appear to be more closely tied to location than either of the environmental factors, as is indicated by the consistent increase in pseudo- R^2 between the GAM with only depth and temperature and that also including latitude and longitude. The abundance appears to be highest for this species between 20 and 40 m bottom depth, a pattern consistent between years. After 1981, the population seems to have expanded its range into northern Bristol Bay, but is not present in the central shelf region, where Alaska plaice predominates. Rock sole commercial catches increased markedly after 1979, seemingly in conjunction with an increase in survey CPUE (Hoff 1989). Also, the GAM abundance estimates (Fig. 7) indicate that rock sole populations have generally increased between 1979 and 1987. Thus, the range expansion of rock sole may be associated with increased abundance.

Yellowfin sole GAMs gave consistently high pseudo- R^2 values, and the results of the permutation tests suggest significance of both depth and (except for 1982) temperature. Commercial catch of yellowfin sole has increased steadily since 1980, and survey CPUE shows consistently high values since 1979, with a peak around 1982 (Hoff 1989). The drop in abundance after 1983, coupled with increases in catch, suggests that this species may be returning to more average levels from the highest abun-

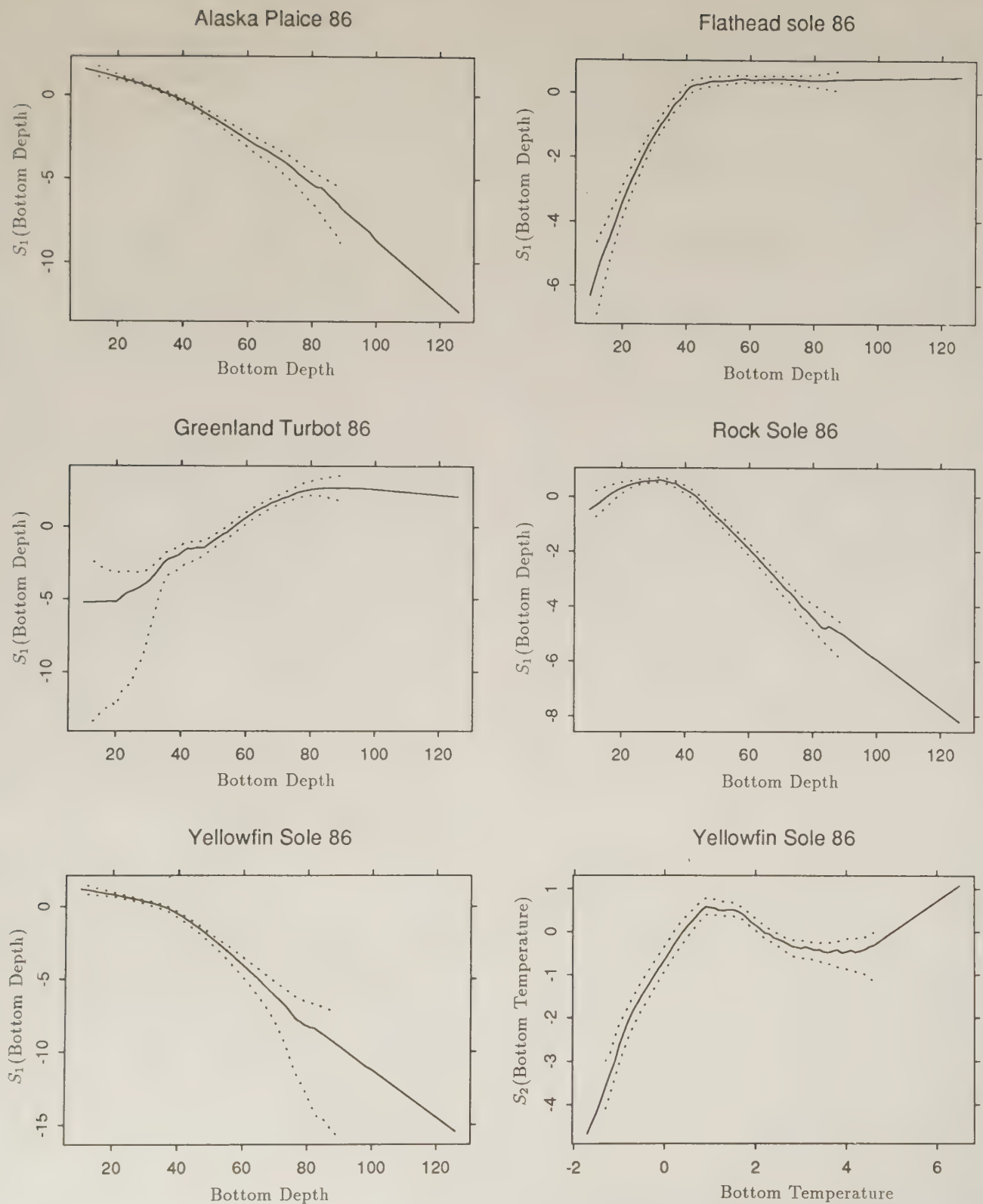


FIG. 5. Plots of the best fitting GAM smooths (solid lines) for each flatfish species for 1986 for bottom depth (m) (denoted S_1) and temperature ($^{\circ}\text{C}$) (denoted S_2 ; yellowfin sole only) with the 90% confidence limits (dotted lines) on these smooths obtained from bootstrap resampling of the original data.

dance levels in recorded history (G. Walters, NWAFC, pers. comm.). The distribution appears to be confined to the central shelf at depths below 40 m, with an additional aggregation in somewhat deeper water in northern Bristol Bay. At the time of the survey, yellowfin sole is spawning (June–September) on the shelf region. Yellowfin sole winters in the outer continental

shelf slope waters and migrates shelfward during the spring (Bakkala 1980). Bakkala (1980) suggested that extensive ice cover may delay the start of spring offshore migration and residual cold water may alter patterns of summer migration and distributions. Therefore, we would expect that an index of ice cover or bottom temperature would strongly influence the dis-

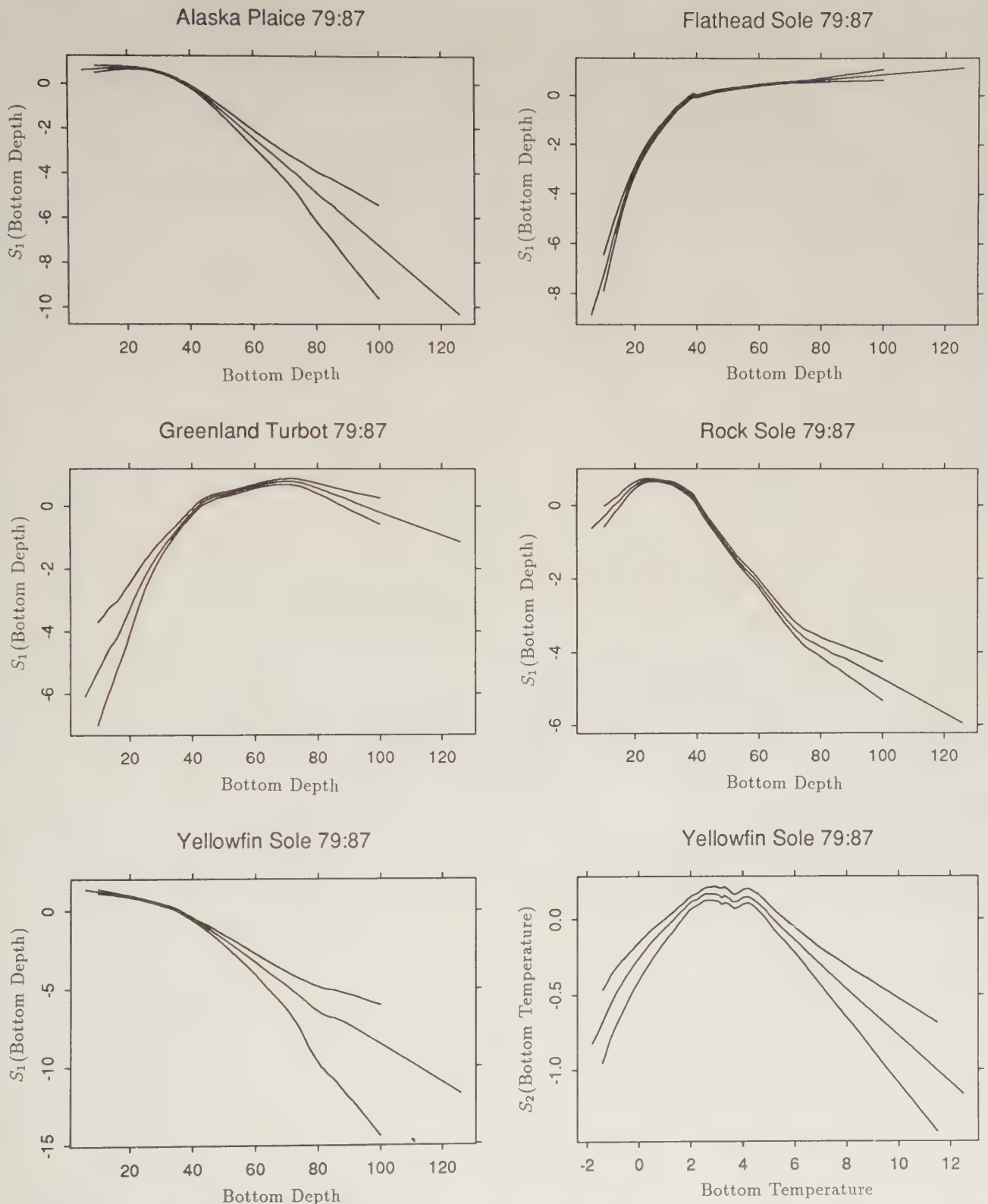


FIG. 6. Plots of the best fitting GAM smooths for each flatfish species for the entire 1979–87 sampling period for depth (m) and gear temperature (°C) (yellowfin sole only) with the 90% confidence limits on these smooths obtained from bootstrap resampling of the original data. The GAM model for this case contains a year effect in addition to the depth and temperature effects.

tribution of yellowfin sole in some years. 1982, a cold year, had smaller than usual aggregations in the midshelf region, which suggests that this species cannot tolerate bottom temperatures less than 2°C. Oddly enough, the temperature–abundance relationship broke down for this year, possibly because the reduced temperature range made discernment of such a rela-

tionship difficult, or possibly because, as suggested earlier, migration patterns were altered for this year. The pooled-year GAM smooths suggest that yellowfin sole prefers a bottom temperature of around 4°C (Fig. 6).

Flathead sole and Bering flounder summer distributions appear to be limited to a depth range greater than 40 m and

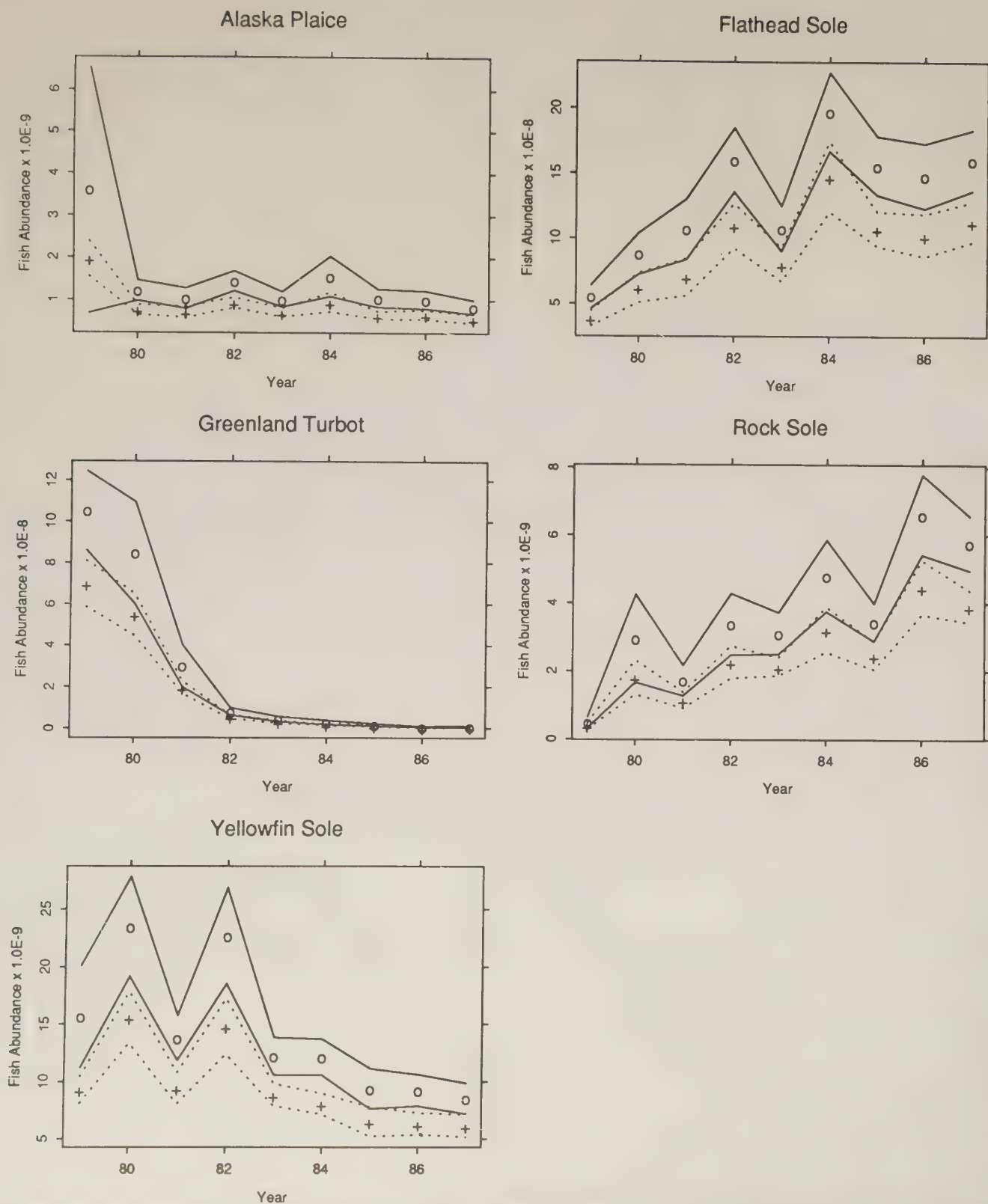


FIG. 7. Results of the GAM estimates for overall abundance for each of the five flatfish species for each survey year compared with the NMFS estimates. The estimates are shown by points. A measure of variability for these estimates is given by deviation lines around the best estimates. Solid lines are used for the NMFS estimates and dotted lines for GAM estimates.

offshore toward the continental slope. Flathead sole spawn from February to May in the midshelf region (Bakkala 1980), yet is found in deeper water in the summer. CPUE from the scientific survey for this species increased steadily from 1979 (Hoff 1989), as is also demonstrated by the generally increasing abun-

dance estimate (Fig. 7), and in 1987, the population appears to have expanded somewhat into shallower shelf areas. These species show the lowest pseudo- R^2 values for GAM fits of all the flatfish species/groups, although the permutation tests showed both depth and temperature to be significant factors.

TABLE 3. Comparison of variation in abundance estimates by species and year between GAM and NMFS stratified sampling procedure. The coefficient of variation is used for the NMFS estimate and the ratio of MAD to median for the GAM estimate.

Year	Method	Alaska plaice	Flathead sole	Greenland turbot	Rock sole	Yellowfin sole
1979	NMFS	0.405	0.081	0.091	0.169	0.142
	GAM	0.106	0.077	0.080	0.125	0.062
1980	NMFS	0.100	0.090	0.145	0.219	0.092
	GAM	0.075	0.091	0.093	0.140	0.072
1981	NMFS	0.117	0.109	0.168	0.130	0.070
	GAM	0.093	0.102	0.075	0.104	0.072
1982	NMFS	0.082	0.077	0.110	0.134	0.092
	GAM	0.065	0.078	0.094	0.105	0.082
1983	NMFS	0.088	0.081	0.134	0.099	0.066
	GAM	0.073	0.081	0.096	0.062	0.055
1984	NMFS	0.153	0.077	0.169	0.110	0.064
	GAM	0.121	0.091	0.107	0.103	0.057
1985	NMFS	0.103	0.072	0.182	0.081	0.093
	GAM	0.067	0.061	0.201	0.084	0.099
1986	NMFS	0.104	0.084	0.164	0.089	0.075
	GAM	0.082	0.079	0.150	0.090	0.076
1987	NMFS	0.096	0.073	0.219	0.070	0.079
	GAM	0.088	0.068	0.160	0.060	0.079

Alaska plaice appears to be restricted to the 20–40 m depth zone (Fig. 6). Over the 20–40 m depth range, the distribution may be random, as is indicated by the relatively low pseudo- R^2 values for the GAMs with only environmental covariates. Alaska plaice CPUE has increased slightly since 1979 and held constant after 1984 (Hoff 1989). The abundance estimates from GAM show abundance decreasing from a high in 1979 (Fig. 7). This species spawns from April to June in continental slope waters and migrates to the continental shelf in June, where its distribution most closely overlaps that of yellowfin sole, although its distribution appears to be somewhat northwest of that species. Of all the species, Alaska plaice has its distribution least related to temperature, and its distribution, unlike that of yellowfin sole, appears unaffected by low bottom temperatures (as in 1982).

Although the GAMs provide believable fits to the data, further investigation of the factors influencing flatfish distribution are needed. Despite the relative year-to-year fidelity of distribution (Fig. 5 and 6), these flatfish species migrate considerable distances over the year in response to changing temperature, food availability, and presumably spawning habitat needs. The survey data present only a snapshot in time, with perhaps insufficient evidence to tease apart the niche definition of these species. Understanding the spatial distinction between the species is a challenge. The GAM work has provided some additional insights and has raised questions that suggest avenues for future research. Some of these questions are life history and physiology questions such as why does yellowfin sole avoid low temperatures, while flathead sole spawns under the ice. Why does flathead sole move from shelf to slope in the spring, while yellowfin sole moves from slope to shelf? Why is the rock sole summer distribution close to the Unalaska peninsula? How consistent from year to year are migration patterns and what triggers them? For some species, we require additional covariates to better define their distribution. This is indicated by having high pseudo- R^2 for the latitude–longitude but not for

environmental factors alone, as with rock sole and flathead sole. Some examples of additional covariates possible are distance from spawning area or from shore, ocean color (a surrogate for primary production), and fishing effort in a region.

Another important question is that of species range and abundance. Does range shrink and expand or remain constant as the overall density changes? We have examined this question in part by looking at the range and changes in abundance of the live species considered, but a longer time series is needed to more effectively examine this question. Finally, further analysis of existing data might shed some light on the effect of size and sex on spatial distribution. The sex distribution of yellowfin sole and rock sole was examined by Hoff (1989) who found some differentiation in yellowfin sole but not in rock sole. Size differentiation of spatial distribution has been postulated for Greenland turbot (Alton et al. 1988). The data are available from the survey to examine this hypothesis and to investigate the existence of size–distribution differences.

GAM is useful at distinguishing major features that influence large-scale spatial trends. It focuses further study on the life history of these fish (e.g. diets, feeding associations, habitat, spawning activity) to better explain spatial phenomena missed by the covariates chosen (available) or taking place on a more local level than GAM can elucidate. The question about how good GAM is can only be answered by having an application in mind. It is good for quantitatively estimating relationships observed in exploratory data analysis. It also smooths out abundance outliers and includes spatial trends in abundance, both of which appear to improve abundance estimates.

Acknowledgements

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Influence of Hydrographic Conditions and Wind Forcing on the Distribution and Abundance of Dungeness crab, *Cancer magister*, Larvae

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The distribution of larval Dungeness crab (*Cancer magister*) was sampled by joint U.S.A./U.S.S.R. ichthyoplankton surveys off the coasts of Washington, Oregon, and northern California involving more than 120 stations from 5 to 360 km offshore and between 40 and 48°N latitude in each of the five years 1981–85. Observed cross-shelf distributions of megalopae were consistent with a mechanism by which diel vertical migratory behavior of the late-stage megalopae in the presence of wind-induced currents results in onshore transport to favorable settlement areas. Total onshore transport for 45 d prior to sampling, estimated as the effects of wind on a passive particle at the surface at night and in the Ekman layer during the day, was correlated with the nearshore megalopal abundance. Mean larval densities for each of the five cruises declined exponentially with time of year of the cruise. This implied (1) an instantaneous mortality rate of $0.066 \cdot d^{-1}$ and (2) that survival is independent of inter-annual variation in environment. Abundance of megalopae was not correlated with station hydrographic data (salinity, temperature, and dissolved oxygen) nor chlorophyll levels (satellite data from the Coastal Zone Color Scanner).

De 1981 à 1985, la répartition annuelle des larves du crabe dormeur (*Cancer magister*) au large des côtes des États de Washington, de l'Oregon et de la Californie nord a été déterminée lors de relevés de l'ichtyoplancton menés conjointement par des chercheurs américains et russes. Des échantillons ont été prélevés à plus de 120 stations à partir de 5 km des côtes jusqu'à 360 km au large, entre 40 et 48° de latitude nord. La répartition observée des mégaloques sur cette étendue de la plate-forme correspondait au phénomène par l'entremise duquel la migration verticale nyctémérale des stades mégaloques avancés en présence de courants dus au vent entraîne le transport vers des fonds côtiers favorables. Il y a corrélation entre le transport total vers les eaux côtières pendant 45 d avant l'échantillonnage, établi comme l'incidence du vent sur une particule passive présente la nuit dans les eaux de surface et le jour dans la couche d'Ekman, et l'abondance des mégaloques dans les eaux côtières. La densité moyenne des larves pendant les cinq croisières d'échantillonnage a diminué de façon exponentielle en fonction du moment de l'échantillonnage. Ceci suggère un taux de mortalité instantané de $0,066 \cdot d^{-1}$ et l'indépendance de la survie sur la variation interannuelle du milieu. L'abondance des mégaloques n'était pas en corrélation avec les données hydrographiques relevées à chaque station (salinité, température et oxygène dissous), ni avec les teneurs en chlorophylle (données-satellite recueillies par balayeur couleur de zone côtière).

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Landings of the Dungeness crab (*Cancer magister*) from northern California to Washington fluctuate by as much as an order of magnitude in apparent synchronous cycles of period 10 yr (reviewed in Botsford 1986; Botsford et al. 1989). Although considerable research has focused on the cause of these cycles, their dynamic basis is still not understood. One of the proposed causes of these cycles is cyclic fluctuations in the physical environment. Correlations between annual popu-

lation data and various environmental variables suggest that the physical environment influences egg and larval stages. Annual catch, considered as a proxy for cohort abundance, has been shown to be correlated with wind stress during the late larval period (Johnson et al. 1986) and sea surface temperature during the hatching period (Wild 1980). Mechanisms proposed are wind-driven transport to a suitable settlement environment and poor egg clutch survival due to high temperatures, respectively.

Because variation in larval survival, transport, and successful settlement could determine the cycles in Dungeness crab abundance, a broad-scale survey of the distribution and abundance of larval crabs would be useful in understanding the population dynamics of the Dungeness crab. The joint U.S.A./U.S.S.R. ichthyoplankton surveys off the coasts of Washington, Oregon,

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and northern California during the years 1981–85 coincided with the late larval phase of the Dungeness crab. More than 120 stations from 5 to 360 km offshore and between 40 and 48°N were sampled in each of the five years. The data from these cruises provide a unique opportunity for comparison of larval distribution to environmental conditions over a broad spatial range.

Possible Environmental Influences

Dungeness crab larvae in this region are subject to oceanographic influences during the first 5 or 6 mo of the year. They hatch near January from eggs carried on the female's abdomen and then progress through five zoeal stages during the next 3–4 mo. They then metamorphose into a megalopal stage and settle to the bottom about 1–2 mo later (Lough 1976; Reilly 1983; Hatfield 1983; Stevens and Armstrong 1985). They settle nearshore in shallow coastal regions and estuaries (Reilly 1983; Stevens and Armstrong 1984, 1985), and few Dungeness crab are found at depths greater than 60 m (e.g. Carrasco et al. 1985).

Both the potential effects of physical conditions and the interpretation of the plankton samples depend on the timing of metamorphosis from the zoeal to the megalopal stage. In 1970, sampling off Newport, Oregon, Lough (1976) first collected megalopae in mid-April and observed that most of the larvae were megalopae by early May. Megalopae first appeared somewhat earlier in central California, around mid-March (Reilly 1983). Hobbs and Botsford (1992) found that metamorphosis had occurred 3 wk earlier off Newport, Oregon, in 1984 than Lough reported for 1970 and 1971. They concluded from 5 yr of samples that most metamorphosis from zoeae to megalopae off Washington, Oregon, and northern California occurred over 2–3 wk at a given latitude and that this peak of metamorphosis occurs either nearly simultaneously at all latitudes or in a manner that proceeds from south to north over less than a month.

One possible environmental effect which we explore here is the potential effect of the local physical and biological environment of the larvae on survival rates and timing of larval development. Laboratory studies indicate that Dungeness crab larvae are sensitive to temperature and salinity concentration (Reed 1969; Gaumer 1971; Lough 1976; Sulkin and McKeen 1989).

A second possible environmental effect explored here is transport of the larval stages to favorable settlement areas. The facts that this study and others report larval distributions extending a considerable distance offshore (Lough 1976; Reilly 1983; Jamieson and Phillips 1988; Jamieson et al. 1989), while successful larvae must settle nearshore (Reilly 1983; Stevens and Armstrong 1984, 1985; Carrasco et al. 1985), imply that cross-shelf transport may be important in returning Dungeness crab larvae to the nearshore environment for successful settlement. The fact that later megalopal stages are found closer to shore than earlier ones (Hatfield 1983; Jamieson and Phillips 1988) also implies onshore transport of this stage. Some investigators have found that in samples taken on cross-shelf transects at a single point on the coast, successive zoeal stages occur progressively farther offshore (Lough 1976; Reilly 1983). They have interpreted this to mean that successive zoeal stages are transported uniformly offshore; hence the megalopal stage would require transport onshore. However, it is also possible that alongshore transport contributed to these observed patterns (cf. Johnson et al. 1986).

Transport of the larvae will depend on the predominant currents in this region. The California Current System off

Washington, Oregon, and northern California consists of the southward flowing California Current and the northward flowing California Undercurrent which surfaces as the Davidson Current in the fall and winter (Hickey 1979, 1989). Flows during the winter are typically southward in the upper layer offshore and northward inshore and beneath the upper layers offshore. After the spring transition the California Current moves inshore and flows are typically southward at the surface and northward below. Wind-driven variations in the alongshore flow are significant (Hickey 1979, 1989; Strub et al. 1987b).

Cross-shelf transport at the surface is almost entirely wind driven, being typically onshore during the fall and winter months and offshore during the spring and summer months. Cross-shelf transport beneath the surface is generally opposite to that at the surface (Hickey 1979, 1989; Strub et al. 1987b). The winds are typically onshore between 35 and 39°N latitude in the winter diverging to the north and south. Above 42°N latitude the winds generally are northward. At some time during March or April the divergence zone below 39°N shifts northward to around 48°N so that the winds are typically onshore and southward above 45°N latitude and increasingly southward below this latitude during the spring and summer. This shift in the divergence zone is referred to as the spring transition and drives the reversal in cross-shelf transport that occurs at this time (Strub et al. 1987a, 1987b).

Wind-forced transport of the larvae would depend on their vertical distribution, for which some observations exist. Researchers have typically found the megalopal stage associated with the surface more than the zoeal stages (Reilly 1983; Booth et al. 1985; Jamieson and Phillips 1988; Shenker 1988; Jamieson et al. 1989; Hobbs and Botsford 1992). Megalopae have been seen during the day clinging to the pleustonic hydroid *Velella velella* (Wickham 1979; Reilly 1983; Shenker 1988) and other flotsam and aggregating in windrows at the surface (Shenker 1988) on cloudy days. There is evidence for diel vertical migration of megalopae with most in the neuston at night (Booth et al. 1985; Jamieson and Phillips 1988; Shenker 1988; Jamieson et al. 1989) but as deep as 60 m on bright days (L. W. Botsford and J. M. Shenker, unpublished plankton data).

From the analyses of diel variation in vertical distribution for 5 yr of data from these U.S.A./U.S.S.R. ichthyoplankton cruises, Hobbs and Botsford (1992) concluded that vertical migratory behavior varies with development stage. Late-stage megalopae migrated vertically on a diel vertical basis, being in the neuston at night and below during the day. The fraction of late-stage megalopae in the neuston was 0.62 ± 0.09 from the hours of 19:00 to 08:00 PST and 0.08 ± 0.02 between 08:00 and 19:00 PST. These results are consistent with those obtained by Booth et al. (1985). Fewer early stage megalopae were in the neuston and they were generally below the neuston at all hours in the one year that the ichthyoplankton cruise coincided with the time of metamorphosis from zoeae to megalopae. In all five ichthyoplankton cruises, zoeae were generally below the neuston at all hours of the day except for 2 or 3 h in the evening (Hobbs and Botsford 1992).

We here test directly for (1) an influence of local environment on larval distribution using hydrographic and chlorophyll data and (2) an influence of wind-induced transport on cross-shelf distribution of crab larvae, using wind data.

Data and Methods

Abundance Data

Five joint U.S.A./U.S.S.R. ichthyoplankton cruises were conducted in 1981–85 (Table 1). The 1984 cruise occurred

TABLE 1. Cruise details for the 5 yr of sampling.

Cruise No.	Period	Research Vessel	Published report
1PO81	9.V–2.VI.1981	<i>Poseydon</i>	Clark 1984
1PO82	3.V–1.VI.1982	<i>Poseydon</i>	Clark 1986
1EQ83	23.IV.–15.V.1983	<i>Equator</i>	Clark and Kendall 1985
1PO84	11.III.–4.IV.1984	<i>Poseydon</i>	Clark and Savage 1988
1BA85	19.IV.–10.V.1985	<i>Mys Babyshkina</i>	Savage 1989a

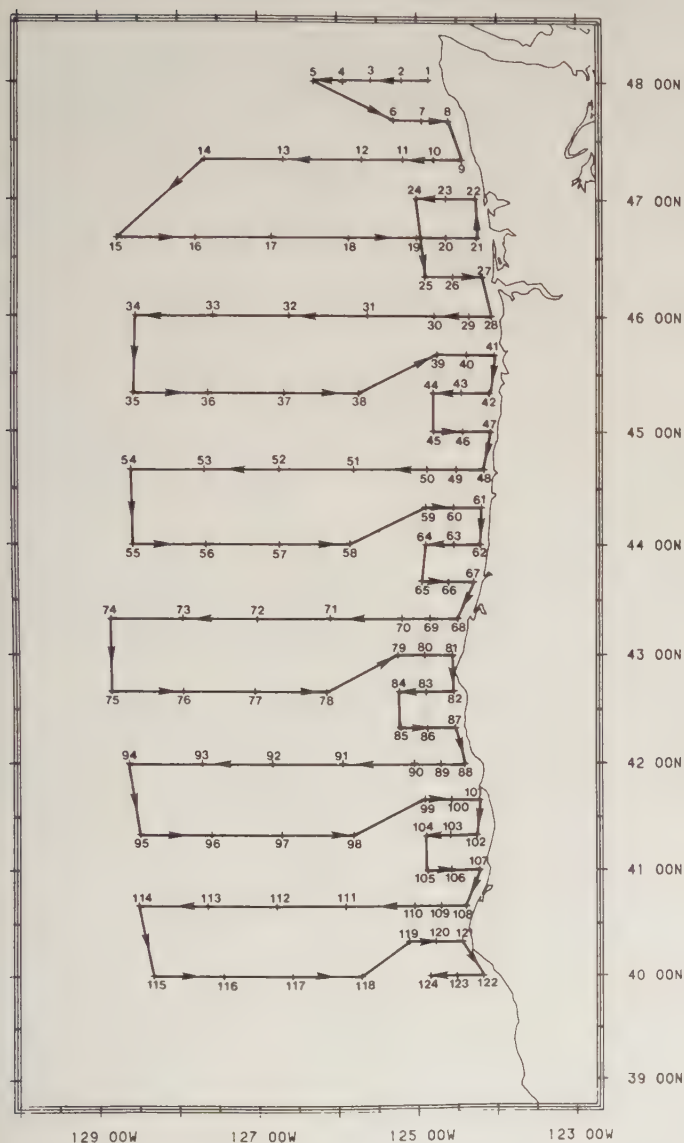


FIG. 1. Typical cruise track. This is the 1983 cruise which began at 48°N latitude in late April and ended at 40°N latitude in mid-May (from Clark and Kendall 1985). The tracks of the other cruises vary from this one only in the order of sampling of nearshore stations at each latitude.

approximately 5 wk earlier than the 1983 and 1985 cruises, which were about 2 wk earlier than the 1981 and 1982 cruises. Each cruise proceeded from north to south and sampled 124 stations from 5 to 360 km offshore and between 40 and 48°N latitude (e.g. Fig. 1). Samples at most stations consist of a neuston tow and an oblique bongo tow, but at some stations only a neuston sample was taken. Neuston tows were made at 2.0 knots ($1.03 \text{ m}\cdot\text{s}^{-1}$) for 10 min using a 0.3-m-high by 0.5-m-wide Sameoto sampler (Sameoto and Jaroszynski 1969)

with a 0.505-mm-mesh net. Bongo tows were standard MARMAP tows (Smith and Richardson 1977) using 60-cm bongo frames and 0.505-mm-mesh nets. Tows were made between the surface and the bottom or a maximum of either 300 or 570 m (depending on the year) of wire out. Flowmeters in the mouths of the nets were used to determine the volume of water filtered.

The ichthyoplankton samples from each cruise were sorted for fish larvae in Poland, and brachyuran larvae were set aside for our use. Samples containing greater than about 60 zoeae were divided using a plankton splitter to generate a subsample of approximately 25–50 zoeae. These zoeae were examined under a binocular dissecting microscope and identified as either *C. magister*, other brachyurans, or unidentifiable (damaged). All megalopae were examined and identified as *C. magister* or other brachyurans (Lough 1975). In both zoeae and megalopae, Dungeness crab was the predominant species. The 1981–83 and 1985 cruises occurred at a time of year when most (95%) of the crab larvae had progressed to the megalopal stage with a few still in late zoeal stages. The 1984 cruise occurred at the time of metamorphosis with most larvae in the north being zoeae and in the south being megalopae.

We estimated local larval abundance and the fraction of larvae in the neuston from the paired neuston and bongo samples using a bias-corrected maximum likelihood method (Hobbs and Botsford 1992). Estimation of megalopal abundance in the 1981–83 and 1985 cruises was based on an assumed diel pattern of migration with a constant fraction of megalopae in the neuston during the day and at night (Hobbs and Botsford 1982). For the few stations where only neuston samples were taken (75 stations, all in the 1982 cruise), we used the estimates of fraction of megalopae in the neuston versus time of day derived in Hobbs and Botsford (1992) as “correction factors” (cf. Jamieson and Phillips 1988; Jamieson et al. 1989) to estimate the abundance of megalopae in the entire water column. Fractions in the neuston were 62% of megalopae in the neuston at night (19:00–08:00 PST) and 8% of megalopae in the neuston during the day (08:00–19:00 PST) (Hobbs and Botsford 1992). We used a similar estimation method to calculate the abundance of zoeae found in the 1981–83 and 1985 cruises, the only difference being that this estimate was based on a 3-h moving average of zoeae to reduce variability (Hobbs and Botsford 1992). In 1984 (the earliest cruise), nearly all of the larvae were found in the bongo samples, and the average abundances of both zoeae and megalopae were sufficiently large that we used only the bongo samples as measures of local abundance for this cruise.

Before conducting statistical tests to determine spatial or temporal covariability between two data sources, it is prudent to first remove any variability introduced by the sampling process. To that end, before attempting to determine whether the spatial distribution of larval data covaried in some way with environmental data, we first removed the effects of the decline in abundance within each year due to natural attrition of the

larvae (i.e. mortality and settlement). Because each of the cruises spanned about 1 mo and began on a different date during the spring with nearly 3 mo separating the beginning of the earliest cruise and the end of the latest cruise (Table 1), the abundance of larvae would be expected to change dramatically over this time due to mortality and settlement. This causes differences in sample abundance that are due only to differences in intraannual timing of the sampling. To remove these differences, we first estimated the rate of decline within the year and then used that estimate to remove that effect.

To estimate the intraannual rate of larval decline from our interannual data, we regressed the logarithm of average larval density (per 10 m²) over each cruise divided by estimated annual egg production (approximated by total (male) catch in the following year, c.f. Hobbs and Botsford 1989) on time of year at the midpoint of the cruise. We divided larval density by estimated annual egg production to remove the effect of the variation in egg production between years.

Since this regression indicated a constant rate of decline through the year, we were able to use the estimated larval mortality rate to remove the effects of that attrition from the abundance data and thereby produce a set of quasi-synoptic abundance estimate (QSAEs). Because the last larval stage is probably the most important one for final settlement, we focused primarily on the megalopae in the later cruises (1981–83, 1985) and adjusted all data for each of those years to what we estimate it would have been if sampled synoptically on May 10 each year. This involved removing the effect of larval decline within each year from the day–night corrected abundance estimates using

$$N(t_0) = N(t) e^{-m(t_0-t)}$$

where $N(t_0)$ is quasi-synoptic abundance on day t_0 (May 10), $N(t)$ is the abundance observed on day t , and m is the instantaneous larval rate of decline. We chose May 10 because it is a date common to all four of the late cruises (Table 1). For the 1984 cruise, we use the average sample date for the cruise (Day of the year (DOY) 83) for t_0 .

Physical Data

Hydrographic data and information on sea state and cloud cover were also taken at each station in the five cruises. These data were measurements of salinity, temperature, and dissolved oxygen taken near the surface by the ship taking the plankton samples. The salinity and temperature data have been analyzed by Savage (1989b).

Chlorophyll abundance at each sample station in each year was from digital images from the Coastal Zone Color Scanner (CZCS). The CZCS, an instrument on the NIMBUS-7 satellite, measures intensity of light reflected from the ocean surface from which chlorophyll abundance can be estimated. Both cloud cover and the low sun angle at higher latitudes early in the year obscure the surface reflectance, making the chlorophyll readings at those points unreliable or nonexistent. We were able to obtain useable chlorophyll readings for approximately one third of the stations. These stations are predominantly within 100 km of the shore and later in the year due to the extensive cloud cover earlier in the year.

We used the U.S. Navy's Fleet Numerical Oceanographic Center (FNOC) meteorological wind fields to compute possible wind-driven transport of the larvae. This wind product provides surface wind velocities twice daily on a grid with 380-km spatial resolution over the entire study period. These are estimated geostrophic winds based on ship and buoy measurements of

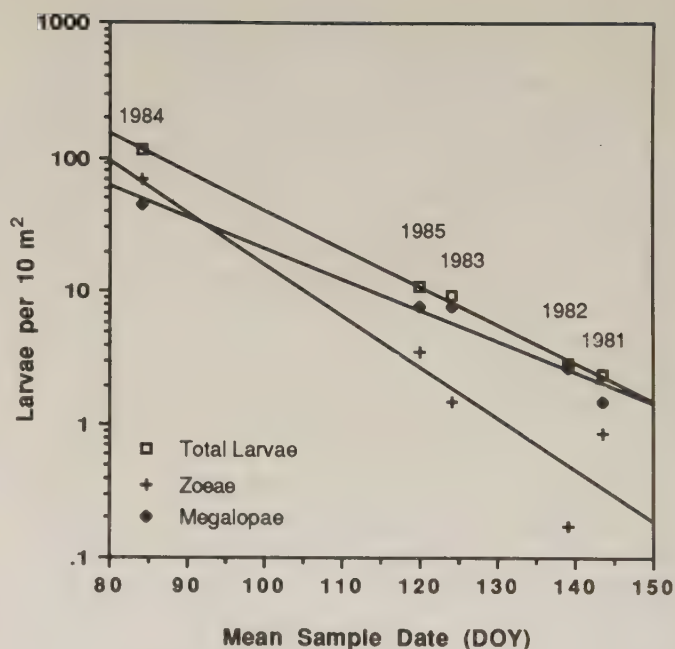


FIG. 2. Larval densities averaged over all locations for each cruise, divided by relative egg production in each year, and plotted against the mean sample date for each cruise. Slopes: total larvae = $-0.066 \cdot d^{-1}$, zoeae = $-0.089 \cdot d^{-1}$, and megalopae = $-0.054 \cdot d^{-1}$.

wind velocity and pressure, as well as model-derived pressure fields. Surface components of these winds are produced by a reduction in velocity and a rotation to simulate boundary layer conditions.

In computing wind-driven transport, we accounted for the fact that megalopae are primarily at the surface at night and below during the day. However, because our knowledge of vertical migration and the influence of wind on surface transport are uncertain, transport was modeled in three ways. We calculated larval transport for the 45-d period prior to sampling for the late cruises (1981–83, 1985) as (1) Ekman transport alone, (2) Ekman transport for 12 h per day and 3% of the wind speed in the direction of the wind for the remaining 12 h, and (3) Ekman transport 12 h per day and 3% of the wind speed with the direction rotated 15° to the right for the remaining 12 h. The first assumes that the megalopae are distributed throughout the upper Ekman layer and does not take into account vertical migration. The latter two account for vertical migration by assuming that the megalopae are distributed throughout the upper Ekman layer during the day but are in the neuston at night. The direction of transport of the megalopae in the neuston is considered to be much closer to the wind direction at the sea surface than the direction of Ekman mass transport, but the actual direction in relation to wind direction is not well known. The two different surface transport directions were an attempt to bracket this uncertainty. We computed Ekman velocity components from

$$V_{EK} = \frac{T_{EK}}{D_{EK} \rho_{water}}$$

where ρ_{water} is the density of seawater, T_{EK} is volume Ekman transport, and D_{EK} is the depth of the wind-driven layer, which was assumed to be

$$D_{EK} = \frac{4.3 W}{\sqrt{\sin \phi}}$$

where W is the wind velocity. Transport over each 12-h period was computed from the value of FNOC wind from that period, interpolated to each degree of latitude from 39 to 49°N, at a point 25 km offshore.

Results

Interannual Temporal Patterns

The estimated overall rate of decline for total larvae is $0.066 \cdot d^{-1}$, or a half-life of about 10.5 d (Fig. 2). This rate includes losses due to mortality of zoeae and megalopae, settlement of megalopae, and advection outside the area surveyed. Because of low variability in estimated female

abundance (coefficient of variation = 0.2), dividing larval density for each year by this factor had little effect on the result. The slope of the regression of adjusted megalopal density ($-0.054 \cdot d^{-1}$) is not as steep as the rate of decline for total larvae because it includes not just losses due to mortality and settlement, but also additions due to metamorphosis from zoeae to megalopae. The rate of decline of adjusted zoeal density ($-0.089 \cdot d^{-1}$) includes both losses due to mortality and losses due to metamorphosis. The fact that the zoeal and the megalopal rates are close to the rate of decline for total larvae suggests that both settlement and metamorphosis rates are less than the mortality rate. Because we have information on only two stages, it is not possible to estimate rates of metamorphosis and

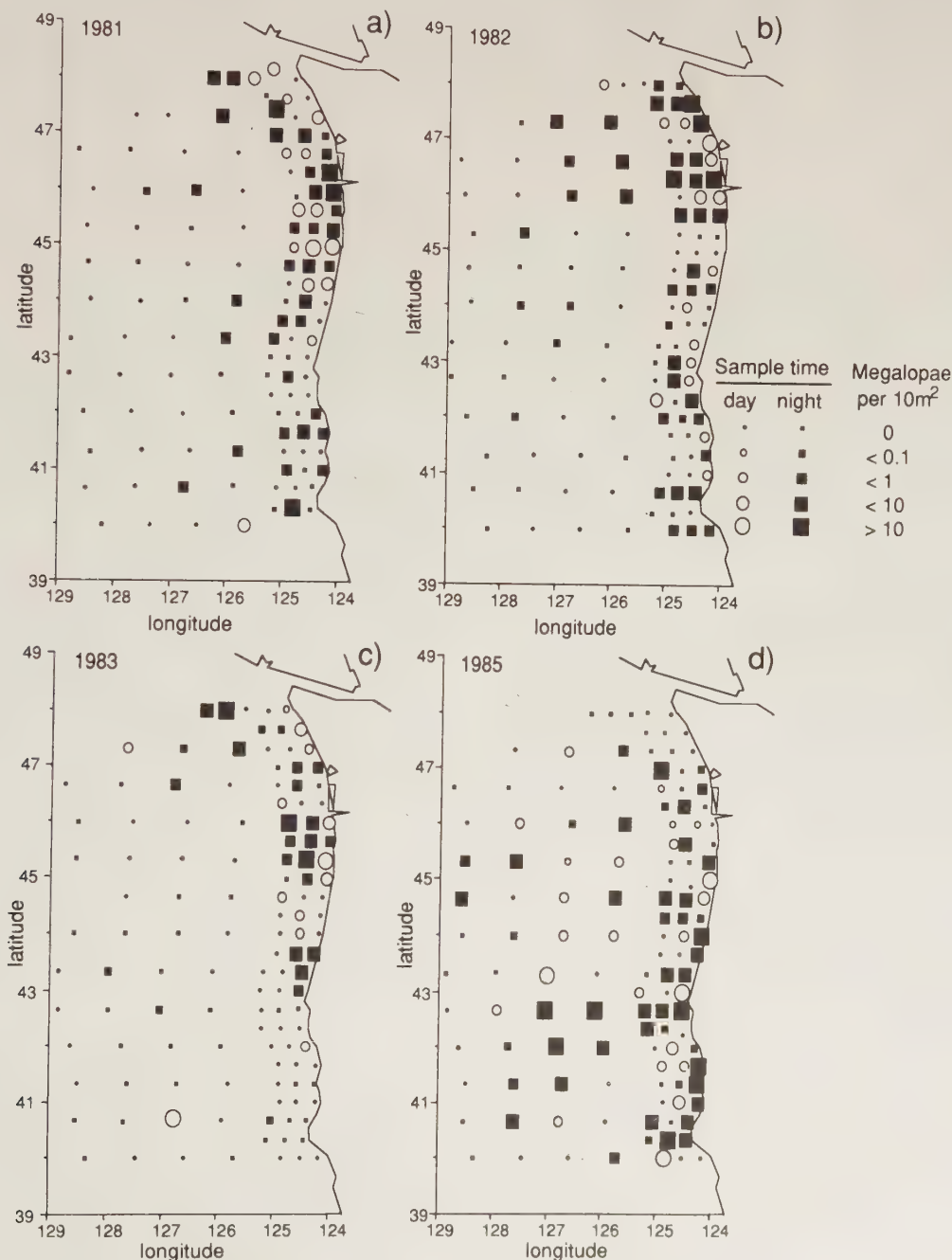


FIG. 3. Quasi-synoptic plots of the corrected megalopal abundances in each of the later cruises (adjusted to May 10) with the estimated abundance represented by the size of the symbol. Day and night samples are indicated by the open circles and solid squares, respectively. (a) 1981; (b) 1982; (c) 1983; (d) 1985.

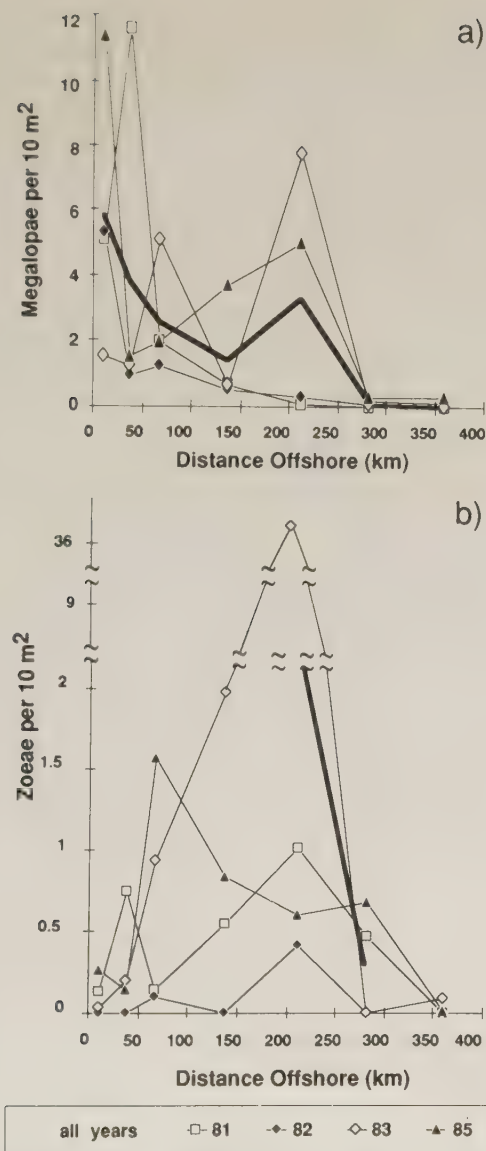


FIG. 4. Average of the corrected larval abundances versus distance offshore for each of the cruises 1981–83 and 1985 and all four years together. (a) Megalopae; (b) zoeae.

settlement. In addition, metamorphosis is most likely not constant with time, but occurs over a small time period so that much of the difference between the rate for zoeae and the rate of megalopae may be due to the fact that the 1984 cruise preceded the time of metamorphosis in the northern latitudes.

Distribution of Larvae

Although the QSAEs of megalopae were corrected for day–night differences (Fig. 3), the daytime samples had a greater variance and a higher probability of a zero estimate when larvae were present. To indicate differences in precision and the probability of false zeros, we differentiated between day and night samples in Fig. 3.

The distributions of megalopae for the two cruises during late April and early May differed substantially from each other, 1985 had more megalopae in offshore samples through all latitudes than 1983 (Fig. 3c, 3d). The distribution for 1983 is skewed toward the north with a single large sample offshore in the south. The megalopae in the two later cruises were predomi-

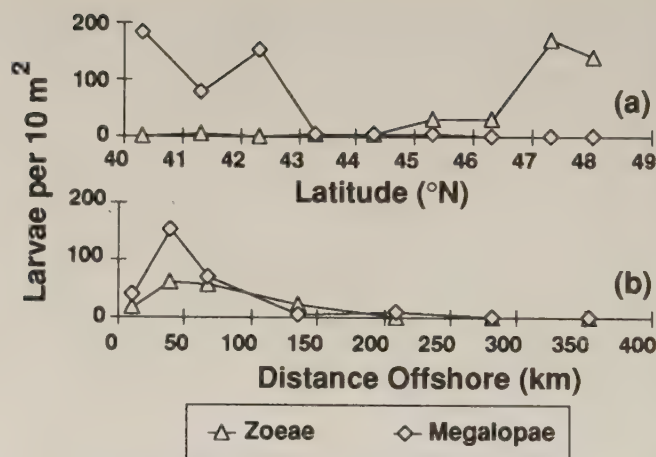


FIG. 5. Average of the bongo tow megalopae and zoeae abundances for the 1984 cruise versus (a) latitude and (b) distance offshore.

nantly nearshore and to the north (Fig. 3a, 3b). The offshore megalopae were also concentrated in the north in 1981 but distributed over all latitudes in 1982.

The QSAEs of megalopae in the 1981–83 and 1985 cruises showed no apparent regular pattern in the distribution of megalopae with latitude; however, cross-shelf distributions were more regular (Fig. 4a). The averaged distribution for all four years shows two peaks, at 10 and 200 km offshore, and very few Dungeness crab megalopae beyond 250 km offshore. Abundance peaked at 75 and 200 km offshore in the 1983 data and both nearshore and at 200 km offshore in the 1985 data. The offshore peak in 1983 resulted from a single large sample in the south (Fig. 3c). Only a single peak nearshore, with very few megalopae beyond 150 km offshore, occurred when samples were taken later in the year (1981, 1982).

Zoeal QSAEs were highest at the extreme latitudes in the earlier cruises (1983, 1985) and at intermediate latitudes in the later cruises (1981, 1982). The cross-shelf distribution of zoeae (Fig. 4b) was dominated by the single large peak in 1983 at 200 km offshore. In the remaining years the zoeae were fairly evenly distributed with lower abundances in the nearest onshore and stations furthest offshore. Significant zoeal abundances were found beyond 150 km in all years.

Because the March–April cruise (1984) coincided with the timing of metamorphosis from zoeae to megalopae, the larvae were predominantly zoeae at the beginning of the cruise in the north and megalopae at the end of the cruise in the south (Fig. 5). Peak densities for megalopae and zoeae were less than 100 km offshore in 1984 with few larvae found beyond 150 km (Fig. 5).

Megalopae Abundance and Local Conditions

There were no significant relationships between log-transformed QSAEs (natural log of $(1 + \text{abundance})$) and the local hydrographic conditions. Megalopae abundance appeared to decline at the extremes of both sea surface temperature and dissolved oxygen concentration; however, there was no apparent visual relationship between megalopae abundance and salinity. Chlorophyll abundance declined exponentially with distance offshore and did not depend on latitude or day of the year. There was no significant relationship between the QSAEs and chlorophyll abundance.

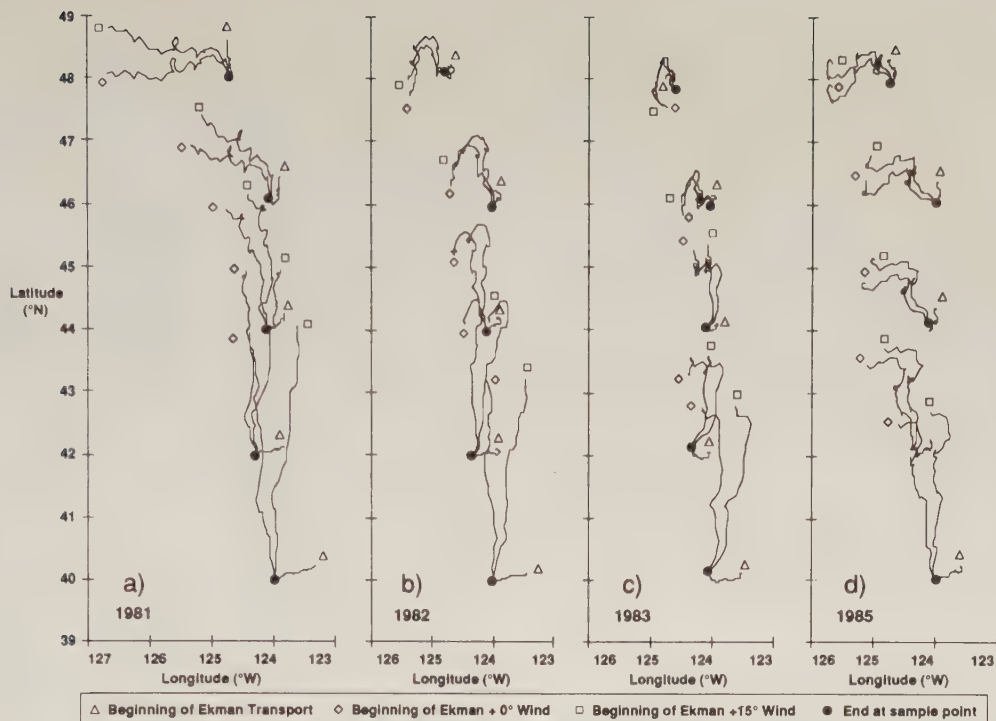


FIG. 6. Wind drift tracks for the 45 d prior to sampling in each of the later cruises ending at the sample point at five latitudes. These were calculated from the FNOC wind field data as (1) Ekman mass transport, (2) Ekman transport for 12 h per day and 3% of the wind velocity for the remaining 12 h, and (3) Ekman transport 12 h per day and 3% of the wind speed, 15° to the right of the wind direction for the remaining 12 h. (a) 1981; (b) 1982; (c) 1983; (d) 1985.

Wind Fields and Cross-Shelf Larval Transport

Wind-induced transport computed in the three different ways showed a consistent latitudinal pattern that varied in magnitude from year to year (Fig. 6). Typically, the onshore component increased with latitude, and the southward component decreased with latitude for methods 2 and 3. Ekman transport only (method 1) was generally southward in the northern latitudes and offshore in the south. Both 1981 and 1982 had almost no north-south transport in the north and transport of 3–4° of latitude in the south. 1983 and 1985 showed a pattern similar to later cruises except that the rapid southward transport in methods 2 and 3 was preceded by a period of onshore transport. The sample dates in these earlier cruises occurred about 3 wk prior to the same latitudes in the 1981 and 1982 cruises, so that an onshore phase at the same time of year would not have shown up in plots for later cruises.

To evaluate the effect on transport of larvae to nearshore habitat, we examined the onshore component of transport by each of the three methods for each year (Fig. 7). The latitudinal pattern of onshore transport remained the same from year to year (with the exception of the far north in 1983), but the magnitude varied. Onshore transport calculated by methods 2 and 3 was generally strong in the north and weak or reversed in the south. Ekman transport only (method 1) was much smaller in magnitude and generally offshore in the south. In the May-June cruises (1981, 1982), method 2 was the only one that resulted in net onshore transport at all latitudes.

There is some correspondence between these patterns and the QSAEs (Fig. 3). For example, onshore transport in the north calculated by both the second and third methods in 1981 was more than twice the 1982 values (Fig. 6a, 6b). This difference was consistent with the greater offshore densities in the north

in 1982 than in 1981 (Fig. 3a, 3b). 1985 had greater onshore transport (calculated by methods 2 and 3) at all latitudes than 1983 (Fig. 7c, 7d). Although 1985 had many more offshore stations with megalopae than 1983, the greatest abundance was found nearshore in 1985 and offshore in 1983 (Fig. 3c, 3d and 4).

To summarize the broadscale patterns, we compared the onshore transport calculated by method 2 averaged over the coast with the average quasi-synoptic densities of megalopae nearshore (<50 km offshore). Onshore transport was greatest in 1981, slightly less in 1985, intermediate in 1982, and low in 1983 (Fig. 8a). The nearshore density of megalopae corrected for time of sampling and relative egg production repeated this pattern almost exactly (Fig. 8b).

Discussion

The consistent decline in annual abundance with time of year indicates a constant larval mortality rate which suggests that the highly variable environment from year to year has little impact on survival through the year. The latter is important because it implies that if the physical environment does have an effect on recruitment, it occurs late in the year, and probably involves transport to favorable settling sites (i.e. nearshore) or survival during or after settlement. However, this conclusion must be accompanied by the caveat that we have only five data points.

This decline in abundance with time of year is especially remarkable in light of the fact that the five years were oceanographically quite different. For example, 1983 was an El Niño year with higher ocean temperatures, different productivity, and different current patterns than our other sample years. It is unlikely that temperature had a direct effect on larvae. The mean sea surface temperature (SST) in 1983 was 1.7°C higher than

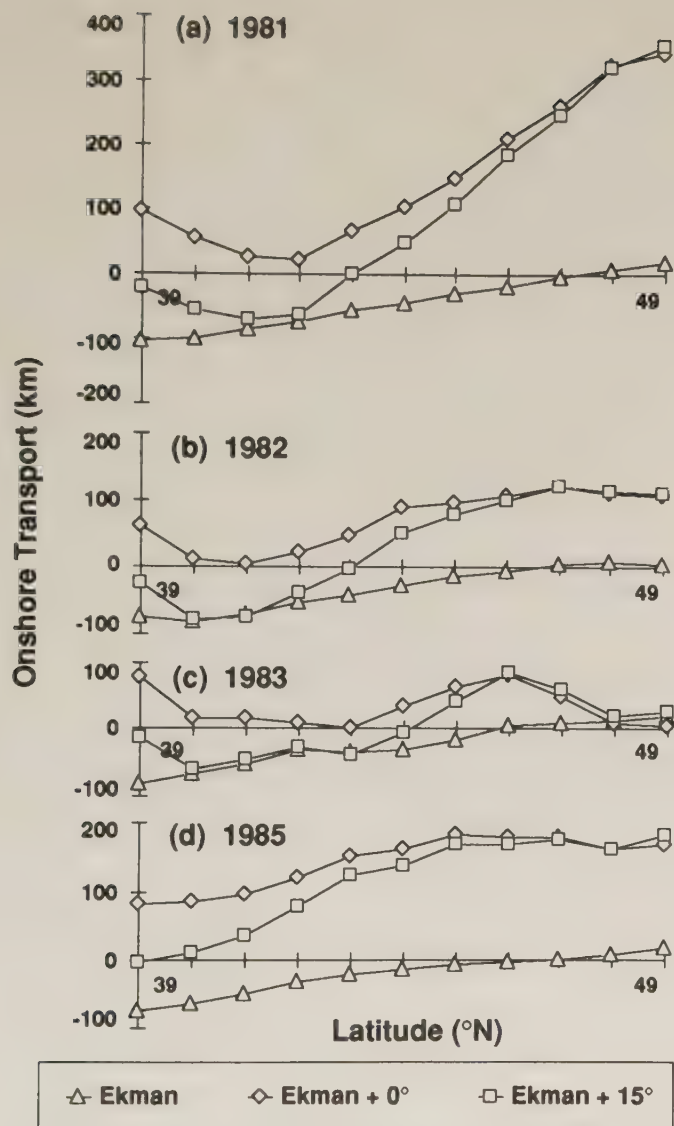


FIG. 7. Total onshore transport versus latitude for the 45 d prior to sampling in each of the later cruises, calculated as (1) Ekman mass transport, (2) Ekman transport for 12 h per day and 3% of the onshore component of the wind for the remaining 12 h, and (3) Ekman transport 12 h per day and 3% of the onshore component of the rotated wind vector (15° to the right) for the remaining 12 h. (a) 1981; (b) 1982; (c) 1983; (d) 1985.

the mean in 1985 in which the cruise spanned approximately the same dates (1983, 12.0°C ; 1985, 10.3°C). Temperatures of 15°C or greater (Lough 1976; Sulkin and McKeen 1989) have been linked to higher mortality in the late-instar zoeae. Although the megalopae in our samples had recently completed this stage, very few stations had temperatures greater than 14°C ; thus even in an extreme year, SST fell within the range that the larvae can tolerate.

Although transport in the direction alongshore could be substantial, larval distributions examined here did not display an interannual variation in north-south distribution that was attributable to interannual differences in the physical environment. During the first 3 mo of the year, moving at average surface current speeds ($9 \text{ km}\cdot\text{d}^{-1}$), passive drifting larvae could be transported as much as 800 miles north by the Davidson Current (Johnson et al. 1986). After the spring transition, larvae could then be transported south a considerable distance by the California Current. The QSAEs for the four late cruises were fairly

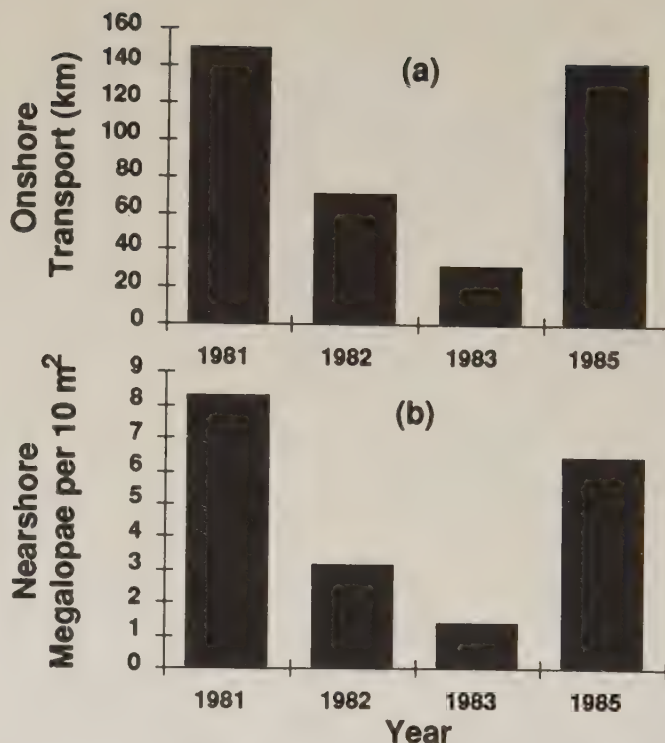


FIG. 8. (a) Total onshore transport for the 45 d prior to sampling in the 1981–83 and 1985 cruises calculated from the FNOC wind field data as Ekman transport for 12 h per day and 3% of the onshore component of the wind for the remaining 12 h; (b) mean megalopal densities nearshore ($<50 \text{ km}$) in the 1981–83 and 1985 cruises.

evenly distributed over latitude (Fig. 3); however, the distributions in the 1984 samples showed a peak of abundances both in the north and in the south (Fig. 5a). The two May–June cruises (i.e. 1981, 1982) did show lower numbers of megalopae in the south relative to the north, but it is possible that significant settlement of megalopae had occurred in the south prior to the sampling time. The distribution of egg production probably did not affect the north-south distribution of larvae greatly, since egg production (when estimated from landing statistics) per kilometre of coast was fairly constant north to south and year to year.

The pattern of cross-shelf distributions was largely consistent with the observation in earlier studies that later stage zoeae are found progressively further offshore (Lough 1976; Reilly 1983) and megalopae first appear offshore and then move rapidly onshore (Hatfield 1983; Jamieson and Phillips 1988; Jamieson et al. 1989). Zoeae were distributed further offshore than megalopae (Fig. 4). In the earlier cruises (1983, 1985), there were more megalopae offshore than in the later cruises (1981, 1983) (Fig. 4a). However, in the very early cruise (1984), there were very few zoeae offshore, indicating that offshore transport may occur later in the year, after the spring transition.

During the late larval period, the distinctive diel vertical migratory behavior of late-stage megalopae coupled with onshore winds provides a mechanism for onshore transport of larvae over distances as great as 300 km in the north and shorter distances in the south. Thus, larvae that are offshore in late spring may return to the nearshore environment in years with strong onshore winds but be stranded in years with weaker winds. The strong relationship between the mean coastwide onshore transport and the mean larval densities nearshore in each year supports this idea. In the southern part of the cruise

area the relatively weak onshore transport in late April followed by a period of southward transport suggest that the timing of the megalopal phase may also be important.

Johnson et al. (1986) found a significant correlation between southward (135–202.5°) component of wind stress averaged over the months of April, May, and June and landings 4 and 5 yr later. That their analysis did not detect a correlation between landings and an eastward component of the winds may be due to two causes. First, our results indicate that the majority of the larvae have moved into the nearshore by the end of May. By including the June winds, which are predominantly southward and stronger than the April and May winds, Johnson et al. (1986) may have biased their results toward a more southerly direction. Second, their analysis was based on winds computed from pressure fields. Halliwell and Allen (1987) have shown that the rotation correction used in these computations is not as great as it should be and that they should be rotated further anticlockwise. This rotational correction varies from 15 to 50° at the latitudes of interest here. Calculation of correlations similar to those of Johnson et al. (1986), but incorporating the improved understanding both of larval phenology and of wind-driven currents, could result in useful insights on the impact of wind forcing on the population dynamics of Dungeness crab.

Although based on only 4 yr of data, our conclusions regarding wind transport are plausible when considered in the context of the correlation between Dungeness crab landings and winds (Johnson et al. 1986) and observations of the importance of transport during critical early life stages of other marine crustaceans. Annual variations in wind fields have been statistically associated with abundance of several spiny lobster species (*Jasus* spp.) in the Tasman Sea (Harris et al. 1988), pink shrimp (*Pandalus jordani*) off the coast of the northwestern United States (Rothlisberg and Miller 1983), and blue crab (*Callinectes sapidus*) in Chesapeake Bay on the east coast of the United States (Johnson et al. 1984). ENSO events which affect both the wind field and circulation on the west coast of Australia are correlated with western rock lobster (*Panulirus cygnus*) settlement and catch records (Pearce and Phillips 1988; Phillips and Pearce 1989). Larvae of both the blue crab and fiddler crab (*Uca* spp.) in Delaware Bay, U.S.A., leave and return to the parent estuary by means of the current system in the mid-Atlantic Bight (Epifanio et al. 1988, 1989). The use of active vertical migration to regulate passive transport during storm surges has been suggested as an important mechanism for return of blue crab larvae into Chesapeake Bay by both field observations (Goodrich et al. 1989) and modeling studies (Johnson and Hess 1990). In a review of transport of the larvae of three coastal crustaceans, *P. cygnus* and *Penaeus merguensis* off Australia and *P. jordani* off the northwestern United States, Rothlisberg (1988) concluded that active control of transport through vertical migration is important both for (1) retention of larvae in rearing grounds and (2) transport to and from the adult habitat.

Our results have implications for the larger question of the mechanisms determining the cycles in abundance in the Dungeness crab fishery. Of the several environmental factors we considered, the timing and strength of onshore winds in the spring appear to be most important in the successful settlement of a larval year class. Equally important is the fact that variations in temperature, salinity, dissolved oxygen, and chlorophyll abundance do not appear to affect larval success. These observations allow us tentatively to narrow our focus to larval transport as the form of environmental forcing in the population dynamics of the crab but do not resolve the question of the relative importance of environmental forcing and density-

dependent effects such as postsettlement cannibalism. If postsettlement survival rates are highly variable or depend on adult densities, then the initial size of the postsettlement juvenile population may have little bearing on resulting adult year class strength (cf. Connell 1985).

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Sublethal Responses of Coho Salmon (*Oncorhynchus kisutch*) to Suspended Sediments

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Servizi, J. A., and D. W. Martens. 1992. Sublethal responses of coho salmon (*Oncorhynchus kisutch*) to suspended sediments. *Can. J. Fish. Aquat. Sci.* 49: 1389–1395.

Underyearling coho salmon (*Oncorhynchus kisutch*) were exposed to sublethal concentrations of Fraser River suspended sediments (SS) in the laboratory. Comparisons with other rivers indicated that Fraser River sediments caused the lowest turbidity for a given SS value. Blood sugar levels (y) were elevated and directly proportional to SS exposure (x) according to $y = 5.79 + 4.23(x)$. Published blood sugar data for adult sockeye salmon (*O. nerka*) exposed to Fraser River SS were in agreement with the linear relationship for underyearling coho. Cough frequency was elevated approximately eightfold over control levels at $0.24 \text{ g SS}\cdot\text{L}^{-1}$. No increase in cough frequency was observed at $0.02 \text{ g SS}\cdot\text{L}^{-1}$. Avoidance was defined by movement to the surface to escape higher SS at depth. Mean avoidance (y) was related to SS by $y = 0.077 + 4.457(x) - 1.547(x^2) + 0.202(x^3)$. Mean avoidance was less than 5% up to the inflection point at $2.55 \text{ g SS}\cdot\text{L}^{-1}$ but rose to approximately 25% at $7.0 \text{ g SS}\cdot\text{L}^{-1}$. Laboratory results indicated that sublethal responses could be expected at naturally occurring SS levels in the Fraser River.

Des saumons coho (*Oncorhynchus kisutch*) de moins d'un an ont été exposés en laboratoire à des concentrations sublétales de matières en suspension (MS) du fleuve Fraser. Des comparaisons portant sur d'autres cours d'eau ont montré que les matières en suspension du fleuve Fraser étaient celles donnant lieu à la plus faible turbidité à valeur égale. Les teneurs sanguines en sucre (y) étaient élevées et directement proportionnelles à l'exposition au MS (x); elles s'exprimaient par la formule $y = 5,79 + 4,23(x)$. Les données publiées sur la teneur sanguine en sucre de saumons rouges (*O. nerka*) exposés à des matières en suspension du fleuve Fraser concordaient avec la relation linéaire déterminée pour les cohos de moins d'un an. La fréquence de la toux était de huit fois supérieure à celle des témoins quand la concentration de MS atteignait $0,24 \text{ g}\cdot\text{L}^{-1}$. Aucune augmentation de la toux n'a cependant été notée à la concentration de MS de $0,02 \text{ g}\cdot\text{L}^{-1}$. Le comportement d'évitement a été défini comme un déplacement vers la surface effectué afin d'éviter la plus forte concentration de MS en profondeur. L'évitement moyen (y) a été relié à la concentration de MS par l'équation $y = 0,077 + 4,457(x) - 1,547(x^2) + 0,202(x^3)$. L'évitement moyen était inférieur à 5% jusqu'au point d'inflexion, situé à $2,55 \text{ g MS}\cdot\text{L}^{-1}$, mais atteignait 25% environ à $7,0 \text{ g MS}\cdot\text{L}^{-1}$. Les essais en laboratoire ont montré que les concentrations naturelles de MS du fleuve Fraser pouvaient donner lieu à des réactions sublétales.

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The Fraser River is one of the world's major salmon (*Oncorhynchus* sp.) producers (Northcote and Larkin 1989) and it also carries a suspended sediment (SS) load which varies with season (Servizi and Gordon 1989). While much of the Fraser River sediment originates from bank erosion in the upper reaches, some tributaries also contribute. In addition, anthropogenic activities may add SS directly or indirectly through alterations to the landscape. Juvenile salmon utilize habitat throughout the Fraser system where they are exposed to a range of SS levels. Acute lethal toxicities for exposure to Fraser River SS have been reported for sockeye (*O. nerka*; Servizi and Martens 1987), chinook (*O. tshawytscha*; Servizi and Gordon 1990), pink (*O. gorbuscha*; Servizi 1990), and coho salmon (*O. kisutch*) (Servizi and Martens 1991).

The objective of this study was to measure sublethal responses of underyearling coho to Fraser River SS by using tests for blood sugar, cough frequency, and avoidance.

Materials and Methods

Test sediment and particle size distribution were described in Servizi and Martens (1987, 1991). Turbidity and SS were

both measured on 115 samples and included data from an earlier study (Servizi and Martens 1991). A nephelometric turbidimeter (HF Instruments Ltd., model DRT 100) was used to measure turbidities. Suspended solids were collected and measured according to Servizi and Martens (1991).

Turbidity and SS of Fraser River sediments were related by the following equation ($p < 0.01$, $r = 0.952$, $df = 113$; Fig. 1):

$$(1) \quad T = 113(SS)^{0.916}$$

where T is nephelometric turbidity units (NTU) and SS is suspended sediment (grams per litre). For various rivers in Alaska, Lloyd et al. (1987) reported that

$$(2) \quad T = 0.44(SS\text{mg})^{0.858}$$

$$(3) \quad T = 1.103(SS\text{mg})^{0.968}$$

where SSmg is milligrams per litre and T is NTU. The expression for Fraser River sediment given in milligrams per litre becomes

$$(4) \quad T = 0.188(SS\text{mg})^{0.916}$$

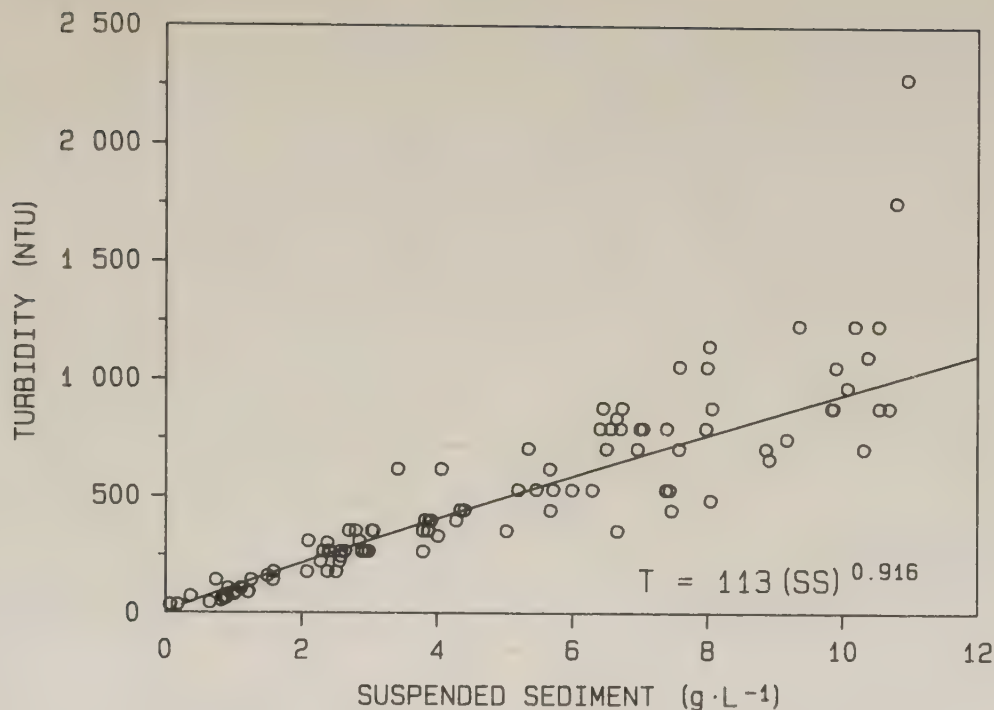


FIG. 1. Relationship between turbidity and SS for Fraser River sediments.

Sigler et al. (1984) reported

$$(5) \quad T = 5.49 + 0.162(SSmg)$$

for water dosed with clay. Comparison among these equations indicates that Fraser River sediments used in biological testing caused the lowest turbidity for a given SS value.

Test fish were Chilliwack River Hatchery coho reared from eggs (Servizi and Martens 1991). Illumination during rearing and testing was via incident daylight from north-, east-, and west-facing windows. Fish were reared at 6–7.5°C and were tested at the rearing temperature. Fish of similar size, as described below, were used in each test. Fish were reared on Oregon Moist Pellet (OMP) but were not fed within 24 h of testing. In all cases the experimental area was screened to prevent disturbance of fish during testing.

Serum glucose was measured in three groups of 10 coho (17.4 ± 2.2 g, 11.9 ± 0.5 cm) following 96 h of exposure to two concentrations of SS and a sediment-free control at 6°C. Fish were confined to cylindrical cages (30×8 cm high) suspended 8 cm below the surface in 217-L conical test vessels. Samples were drawn twice daily at the top of cages for measurements of SS. At 96 h the cages were quickly transferred one at a time to an anaesthetic bath (2-phenoxyethanol, $0.5 \text{ g} \cdot \text{L}^{-1}$). Blood was collected in micro serum separators immediately following severance of the caudal peduncle. Serum glucose was measured by the hexokinase enzymatic procedure (Anonymous 1974).

A total of 93 coho (20.1 ± 5.5 g, 12.3 ± 1.1 cm) were exposed to four SS concentrations and a control for measurements of cough frequency at 6°C. The numbers tested at each concentration are reported in Table 1. Fish were confined to individual cages ($15 \times 3 \times 4$ cm) submerged at a depth of 8 cm in 35-L test vessels (Servizi and Martens 1991) during measurements of cough frequency. Samples for SS were collected twice daily at the top of cages.

Coughs were monitored using a buccal cannula (Saunders 1961) connected via polyethylene tubing (Clay-Adams PE60 Intramedic) to one of two physiological pressure transducers

(model P23BB, Statham Laboratory) and then to a recorder (model 321, Sanborn dual-channel carrier amplifier). Fish were monitored by attaching the free end of the polyethylene tubing to one of the two transducers, recording, disconnecting, and connecting the next specimen in turn. Generally, fish were handled in groups of four in the following way. Four freshly cannulated fish were placed in cages and rested for 18 h in sediment-free water, when baseline ventilation measurements were made. Two of these fish were transferred in their cages, submerged in a basin of water, to a SS concentration where they rested until ventilation measurements were made, while two fish served as controls. Control cages were lifted, also submerged in a basin of water, and replaced to simulate transfer. Ventilation rates were measured after transfer (real and simulated) according to the schedule in Table 1. For each fish, the baseline and experimental measurements were made on the same transducer and the same recorder channel. Following transfer in their cages, fish were allowed to rest for approximately 1 h before baseline or experimental ventilation was measured. On the average, ventilation was measured for approximately 11 min and was about equally divided between baseline and experimental conditions. Coughs were identified as prominent spikes among uniform pressure recordings of ventilation (Schaumburg et al. 1967). Elapsed time between coughs was used to calculate cough frequencies.

Avoidance tests used 30 fish (1.0 ± 0.1 g) in each 35-L test vessel (Servizi and Martens 1991). Avoidance was based upon the tendency of coho to swim at the surface to avoid higher SS at depth. Twenty-five SS concentrations and five controls were tested at 7°C. The same operator made all observations but only after several days of practise to assure objectivity. Observations commenced within 10 min of transferring fish to test vessels and continued for 96 h. The observer looked at the water surface and immediately counted all the fish seen. Owing to turbidity, only fish within approximately 1 cm of the surface could be seen in experimental vessels. In controls, the observer

TABLE 1. Mean cough frequencies (SE, maximum) of underyearling coho prior to and during exposure to Fraser River SS. Means followed by the same letter are not significantly different.

Group	No.	Baseline coughs·min ⁻¹	SS (g·L ⁻¹)	Turbidity (NTU) ^a	SS exposure	
					1 h (coughs·min ⁻¹)	24 h (coughs·min ⁻¹)
A	30	0.14a (0.05, 0.81)	0.00	0	—	0.19a (0.05, 0.94)
B	19	0.17a (0.06, 1.00)	0.02	3	—	0.19a (0.06, 0.78)
C	10	0.27a (0.13, 0.80)	0.24	30	—	1.51b (0.36, 3.32)
D	18	0.09a (0.04, 0.45)	2.46	260	5.31d (0.171, 11.7)	3.32c (0.82, 11.70)
E	16	0.13a (0.05, 0.67)	6.78	666	6.70e (0.84, 13.20)	—

^aCalculated from equation 1.

counted only fish within approximately 1 cm of the surface. Fifty observations were made of each test vessel at approximately equally spaced intervals during each 7.5 h working day. The proportion of fish at the surface was calculated for each observation and the mean calculated for the 200 observations made at each concentration. All 6000 observations were used to calculate analysis of variance and 95% confidence intervals. Samples for SS measurements were collected twice daily at 8 cm depth. Two hundred and forty SS measurements were made during avoidance testing and these were used to calculate 95% confidence intervals for SS. A suspended solids gradient was based upon 199 measurements at depths from 2 to 25 cm in identical test vessels without fish present.

Temperatures in test vessels were maintained by water bath and were measured daily. Dissolved oxygen exceeded 90% of saturation in all cases. Water from Cultus Lake was used for rearing and for dilution water (Servizi and Martens 1991).

Analysis of variance was computed by the GLM procedure (SAS Institute Inc. 1985). We compared means using Duncan's multiple range test (SAS Institute Inc. 1985) and the Tukey-Kramer test (Sokal and Rohlf 1981).

Results

Mean blood sugar of underyearling coho was elevated above control levels following 96 h of exposure to SS (Fig. 2). Mean glucose levels at 0, 0.53, and 1.36 g SS·L⁻¹ were not statistically different by ANOVA (GLM) but the regression between glucose (y , millimoles per litre) and SS (x , grams per litre) was significant ($p < 0.05$, $r = 0.384$, $df = 27$):

$$(6) \quad y = 5.79 + 4.23(x).$$

Cough frequencies were measured for cannulated coho in the four exposure groups and the control before and during SS exposure (Table 1). Prior to SS exposure, mean cough frequencies ranged from 0.09 to 0.27 cough·min⁻¹ but there were no statistical differences among the groups. The weighted mean was 0.15 cough·min⁻¹. Ninety percent of the fish had a baseline cough rate of 0.50·min⁻¹ or less. The mean cough frequency of Group A (control) was unchanged after 24 h as was that of the 0.02 g SS·L⁻¹ exposure group (B). However, after 24 h of exposure to 0.24 g SS·L⁻¹ or more, mean cough frequencies were elevated above control values (ANOVA, GLM, $p < 0.05$). In addition, cough frequencies increased with SS concentration to a maximum observed value of 13.20·min⁻¹ measured in 6.78 g SS·L⁻¹. One hour after exposure to 2.46 g SS·L⁻¹, mean cough frequency was significantly increased to 5.31·min⁻¹ but declined to 3.32·min⁻¹ at 24 h (t -test, $p < 0.05$).

When coho were kept in clear water without confinement to a particular depth, they usually schooled just above the screen (20 cm depth) and were seldom seen at the surface. However, when coho were exposed to SS in test vessels, their normal behaviour was altered within minutes and some fish swam at the surface at intervals apparently to take advantage of lower SS. Evidence of a SS gradient was confirmed by measurements. Quadratic regression of the data yielded equation 7 ($p < 0.01$, $r = 0.693$, $df = 196$):

$$(7) \quad y = 100 + 2.6(x) + 0.1(x^2)$$

where y is percent of SS at the surface and x is depth (centimetres). For example, according to equation 7, SS at 18 cm depth is estimated to be 170% of the value at the surface. Typically, fish could only be seen in the turbid waters when their backs were within approximately 1 cm of the surface. The fish avoided the jet of recirculated water in exposure vessels and selected eddies at either side of the jet. The fish which could be seen were often within 1 cm of each other. There was no evidence of acute oxygen deprivation, such as gulping, among fish observed at the surface. We interpret swimming at the surface in turbid water as demonstrating avoidance of higher SS at depth. Close observation indicated that individual fish did not stay at the surface constantly, but appeared at the surface for minutes and then submerged. As one fish submerged, another would often surface at a different point. Percent avoidance was calculated for each observation and ANOVA (GLM) of all avoidance and SS data yielded $p < 0.005$, confirming that significant differences exist between means. Linear and third-order polynomial regressions yielded r values of 0.940 and 0.966, respectively. In addition, visual comparison confirmed that the polynomial gave a better fit to the data (Fig. 3). Accordingly, we concluded that avoidance was represented by equation 8 ($p < 0.01$, $r = 0.966$, $df = 28$):

$$(8) \quad y = 0.077 + 4.457(x) - 1.547(x^2) + 0.202(x^3)$$

where y is percent avoidance and x is grams SS per litre measured at 8 cm depth. Figure 3 suggests low-level avoidance to the inflection point (defined by $d^2y/dx^2 = 0$) at 2.55 g SS·L⁻¹ (NTU = 270). For SS beyond this value, the slope of the curve (dy/dx) increased steadily, passing through 1:1 at 3.45 g SS·L⁻¹, and avoidance rises to about 25% at 7.0 g SS·L⁻¹. Equation 8 predicts a 96-h EC50 for avoidance at 8.5 g SS·L⁻¹ (EC50; median effective concentration causing a response for 50% of fish). The narrow 95% confidence intervals for SS in Fig. 3 indicate low temporal variability of exposure conditions. Confidence intervals for SS ranged from 0.01 to 0.50 g·L⁻¹ and are typical for all the experiments reported herein and compare favourably with SS data previously reported for this apparatus and methodology (Servizi and Martens 1991).

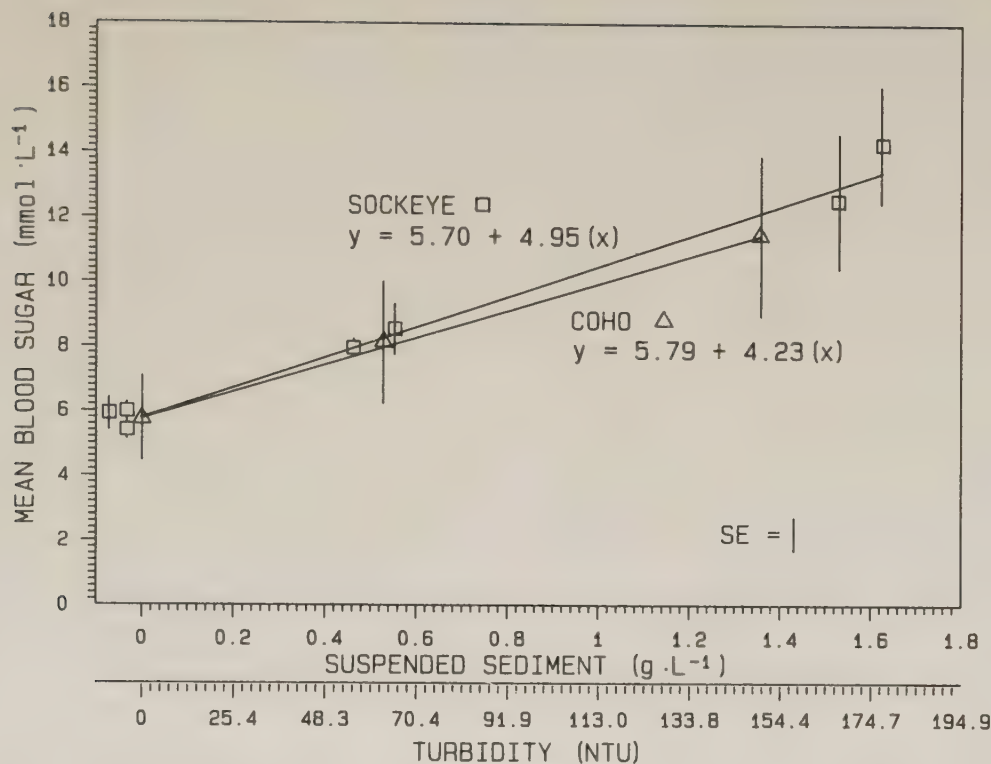


FIG. 2. Responses of blood sugar to SS exposure for underyearling coho (this study) and adult sockeye (from Servizi and Martens 1987).

Discussion

Increased blood sugar was one of the responses of underyearling coho to SS. Similar increases in blood sugar were reported for adult sockeye exposed to Fraser River SS for 9 and 15 d (Servizi and Martens 1987) at temperatures in the range 7.5–14.5°C (Fig. 2). Mean blood sugar levels for sockeye exposed to 1.53 and 1.63 g SS·L⁻¹ were different from those at 0.55 and 0.46 g SS·L⁻¹ and from controls (ANOVA, GLM, $p < 0.05$) and regression yielded equation 9 ($p < 0.01$, $r = 0.689$, $df = 59$):

$$(9) \quad y = 5.70 + 4.95(x).$$

Equation 9 differs only slightly from equation 6 (coho blood sugar) and for most purposes they could be considered equal. Mean glucose levels were not statistically different for coho exposed to SS but the regression was significant ($p < 0.05$). Sokal and Rohlf (1981) noted that the regression test is more powerful than ANOVA and a significant regression is sometimes found when means change only slightly, as is the case for coho mean blood sugar. Elevation of blood sugar is cited as a secondary stress indicator (Wedemeyer et al. 1984). McLeay et al. (1987) reported increases in blood sugar and blood sugar variance among Arctic grayling (*Thymallus arcticus*) exposed to SS for 24 and 96 h but no mathematical relationship was obtained, since increases were highly variable. These authors concluded that the 24-h EC50 was less than 0.05 g·L⁻¹ for organic sediment (placer mining "overburden"). According to equation 6, 0.05 g Fraser River SS·L⁻¹ would elicit only a 3.6% increase in mean plasma glucose after 96 h. This change would not be detectable from control values. An increase in blood sugar variance among groups of salmonids was also considered a stress response (Wedemeyer and McLeay 1981). It is noteworthy that variance, in the form of standard error, increased with SS for coho and sockeye (Fig. 2). For under-

yearling coho, variance was noticeably increased at the 0.52 g SS·L⁻¹ exposure level. This value is a 17% increase over the baseline and is 2.4% of the 96-h LC50 for coho in Fraser River SS at 6°C (Servizi and Martens 1991). Redding et al. (1987) used cortisol levels to detect primary stress responses among yearling coho exposed to suspended topsoil in the 0.3–0.6 and 2.0–4.0 g·L⁻¹ ranges. Although cortisol levels were initially elevated fivefold, they decreased within 96 h, indicating physiological compensation.

The foregoing comparisons indicate that blood sugar consistently responds to the stress induced by sublethal SS exposure. For the study reported herein the relationship between blood sugar and Fraser River SS is linear up to 1.4 g·L⁻¹. However, beyond this range, blood sugar may rise faster than linear until toxic actions impair this response. This speculation is based on our analysis of published data (McLeay et al. 1983) which indicates that blood sugar (y , millimoles per litre) and the toxic substance pentachlorophenol (x , micrograms per litre) are related exponentially ($y = 3.73e^{0.0164x}$) over a 50-fold range for Arctic grayling.

Response to a stressor is dependent on environmental factors such as duration of exposure and temperature. Blood sugar values responded equally for underyearling coho and adult sockeye exposed to Fraser River SS but exposure times and temperatures differed for the two species. Furthermore, adult sockeye were undergoing physiological changes associated with maturation. Given these differences, the nearly identical equations for underyearling coho and adult sockeye responses may be coincidence. Further testing would be required to resolve the question of coincidence.

The maximum cough frequency observed for coho exposed to SS was 13.20·min⁻¹ (Table 1). This maximum is slightly less than the 15–20 cough·min⁻¹ maximum estimated for rainbow trout (*O. mykiss*), no matter what the extent of stimulus

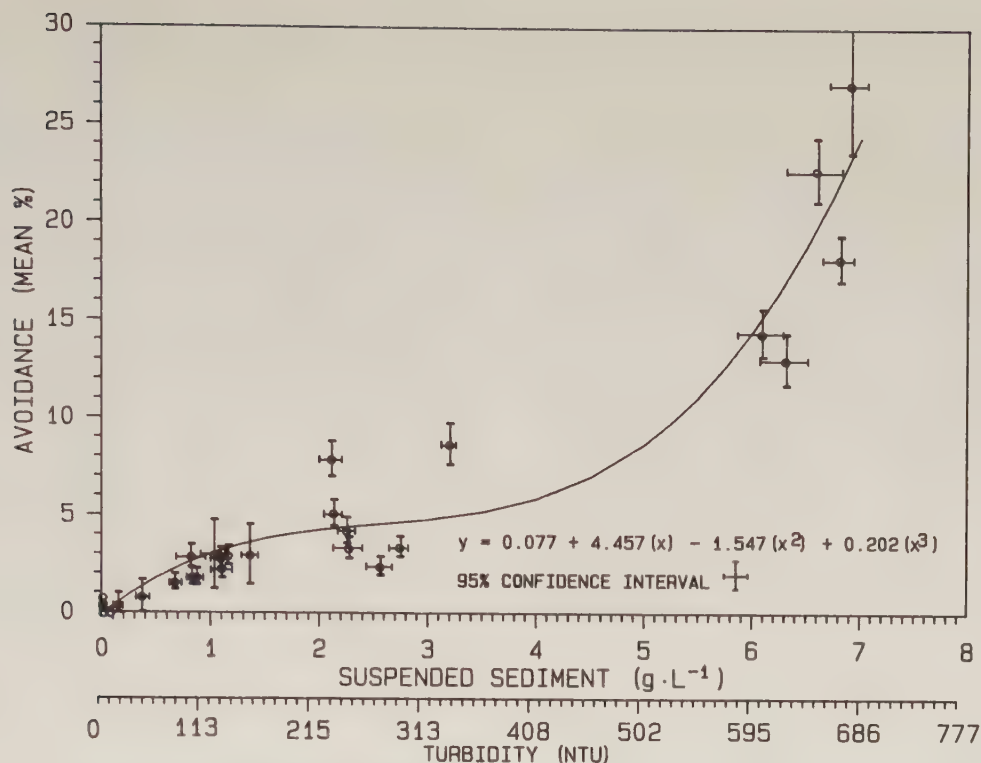


FIG. 3. Avoidance of SS by underyearling coho calculated from the percentage of the population observed at the surface during 96 h.

(Bass and Heath 1977). Mean cough frequency was less at 24 h than at 1 h during exposure to $2.46 \text{ g SS} \cdot \text{L}^{-1}$. This result is consistent with reports of an overnight decrease following an initial rise in cough frequency during exposure to a stressor. Specifically, cough frequencies decreased for sockeye (Davis 1973) and rainbow trout (Walden et al. 1970) after overnight exposure to bleached kraft mill effluents.

Increased cough frequency has been reported for fish exposed to various chemicals (Heath 1987) and effluents (Walden et al. 1970; Davis 1973) but there are limited observations for exposure to SS. Cough reflex is the mechanism by which fish expel foreign matter from gills (Fry 1957). Bams (1969) reported that sockeye alevins used the cough reflex to clear buccal cavities of suspended particles. MacLeod and Smith (1966) made an early attempt to quantify cough reflex when they made visual counts to calculate cough frequencies for fathead minnows (*Pimephales promelas*) exposed to pulp fibers. They reported that coughing was elevated within minutes following exposure to 25 ppm pulp fibers. In our tests, $0.02 \text{ g SS} \cdot \text{L}^{-1}$ (20 ppm) did not cause an increase in cough frequency at 24 h (Table 1). The difference in response may be related to the nature of the suspended particles and species differences. Visual counts of "gill flaring" indicated that cough frequency was significantly elevated when underyearling coho were exposed to SS (gravel pit fines, largely $0.02\text{--}0.06 \text{ mm}$) for 1–48 h at 30 NTU (Berg and Northcote 1985). More than 90% of particles in Fraser River SS were 0.05 mm and smaller, based upon geometric mean diameter (Servizi and Martens 1987, 1991). A turbidity of 30 NTU is equivalent to about $0.24 \text{ g Fraser River SS} \cdot \text{L}^{-1}$ (equation 1), which caused a significant increase in cough frequency at 24 h. These results are supportive of a threshold between 3 and 30 NTU for elevation of cough frequency.

Although swimming at the surface has been reported during exposure to SS for Arctic grayling (McLeay et al. 1987) and

underyearling sockeye (Servizi and Martens 1987), our results are the first attempts to quantify this behaviour. The tendency of coho in control vessels was to remain submerged several centimetres below the surface. Less than 1% of the fish were observed at the surface in clean water. At SS exceeding $0.3 \text{ g} \cdot \text{L}^{-1}$ (37 NTU), coho exhibited first signs of avoidance behaviour in the vertical plane. This point is 1.3% of the 96-h LC50 (Servizi and Martens 1991) and is close to $0.24 \text{ g SS} \cdot \text{L}^{-1}$, at which significant elevation of cough frequency occurred. Thus, avoidance may be a response to the stress associated with increased cough frequency. Mean avoidance was less than 5% up to the inflection point at $2.55 \text{ g} \cdot \text{L}^{-1}$ (NTU = 269). Continuous increase in the slope of the avoidance curve as SS increase beyond the inflection point (Fig. 3) may be an indication that the need for relief from SS stress increasingly overcomes the preference to stay submerged. Each time coho swim near the surface in a natural setting there is risk of avian predation (Peterson 1982). If the behaviour observed in the laboratory occurred in nature, avian predation may cause a significant loss.

Reports of salmonid avoidance behaviour in the horizontal plane can be compared with the three sublethal responses observed herein. Sigler et al. (1984) reported emigration of juvenile coho and steelhead (*O. mykiss*) from rearing channels containing 11–49 NTU. These authors suggested that this emigration was evidence that turbidity was stressful to the fish. We estimated that the threshold for avoidance in the vertical plane was 37 NTU. Our results for elevation of blood sugars, cough rate, and avoidance response support the contention by Sigler et al. (1984) that turbidity was stressful in the range 11–49 NTU. Bisson and Bilby (1982) reported a 13% decrease ($p < 0.05$) in numbers of naive coho in the turbid side of a horizontal trough at 70 NTU. On the other hand, in the vertical plane, mean avoidance was only 2% at 70 NTU (Fig. 3). This com-

parison suggests that coho may be more inclined to move laterally than to the surface to avoid stresses imposed by SS. Avoidance in the vertical plane may be attenuated by the preference shown for depth in clear-water controls.

Newcombe and MacDonald (1991) have proposed a ranked response, derived from a stress index, as a means of predicting sublethal and lethal effects on salmonids caused by SS episodes of known intensity. The model is based upon episodes ranging from 1.2 min to 361 d in duration and SS concentrations from 0.7 to 207 000 mg·L⁻¹. The ranking is calculated from an equation based upon the natural logarithm of the product of exposure concentration (milligrams per litre) and duration (hours). The model imposes no constraints on exposure duration or SS concentration. The stress index model predicts that increased coughing would occur at 0.202 and 0.008 mg SS·L⁻¹ after 1 and 24 h, respectively. Our results indicate that coughing rate was not affected at 20 mg·L⁻¹ and was elevated at 240 mg·L⁻¹ (Table 1). The stress index model predicts avoidance in the range 4.7–18.2 mg SS·L⁻¹ at 10 min and at 0.032 mg·L⁻¹ after 24 h, but we found that mean avoidance in the vertical plane did not exceed threshold values until SS exceeded 300 mg·L⁻¹ (Fig. 3). The model also predicts physiological stress (elevated blood sugar) at 27.7 mg SS·L⁻¹ after 96 h. An SS value this low has no detectable effect on blood sugar according to our equations 6 and 7. For the cases cited above, the stress index model predicts SS values one to four orders of magnitude below the values at which sublethal effects were observed. The stress index model also predicts 40–60% mortality during 96 h at 6900 mg·L⁻¹. This concentration was the highest used in avoidance tests (Fig. 3). Even if the test fish stayed at the surface (1 cm) where mean SS would have been 5600 mg·L⁻¹ (equation 8) the stress index model predicts 20–40% mortality. However, no mortalities occurred during avoidance tests at 6900 mg·L⁻¹ or any other concentration. Furthermore, the mortality ranges predicted above by the stress index model compare poorly with the 96-h LC50 for coho (23 000 mg·L⁻¹) exposed to Fraser River SS at 7°C (Servizi and Martens 1991). We believe that the use of open-ended exposure time and SS concentration without regard to threshold effect levels or other factors such as temperature and fish size causes the model to be an unreliable predictor of sublethal and lethal effects.

Underyearling coho responded to SS by increasing blood sugar and cough frequency and by avoiding SS at depth. Could sublethal responses be expected in the Fraser River, one of the world's major producers of salmon? Coho bound for the sea use the Fraser River in spring when typical SS are in the 0.3–0.6 g·L⁻¹ range and occasionally may exceed 1.0 g·L⁻¹ according to records for 1967–87 (Servizi and Gordon 1989; Anonymous 1985, 1988, 1989). There is no reason to believe that the SS regime varied historically from these values. Coho smolts spend 1–25 d traversing the Fraser River from the various natal tributaries (C. Levings, Department of Fisheries and Oceans, West Vancouver, B.C. V7V 1N6, pers comm.). The highest SS value is about 5% of the 96-h LC50 for underyearling coho exposed to Fraser River SS. Thus, outright mortality would not occur. According to Fig. 2 and 3 and Table 1, SS levels typical of the Fraser River could be expected to elicit sublethal responses. In fact, blood sugar and cough frequency are probably elevated over baseline levels at the SS concentrations which occur in the Fraser River. However, coho could avoid high SS by travelling in the upper layers of the river where SS are least (Anonymous 1985, 1988, 1989). Outmigrant juvenile Pacific salmon showed strong preferences for

surface waters in the lower Fraser River where approximately 63% occurred in the upper 25% of the water column (0–1.4 m) (Anonymous 1981). While average and maximum SS in the Fraser River may evoke sublethal responses among juvenile salmon, the historical evidence for major salmon runs suggests that the response levels probably did not exceed homeostatic capacity.

In this paper we have reported a relationship between SS and turbidity (equation 1) and compared it with regressions reported in the literature for rivers in Alaska (equations 2 and 3) and a natural water dosed with clay (equation 5). Fraser River SS produced the least turbidity for a given level of SS. Since turbidity is based on light scattering, and very fine particles would scatter more light than coarser particles of the same total weight, it is probable that Fraser River SS particles are larger than those referenced. Particle size has biological implications, since acute lethal tolerance of SS by juvenile sockeye decreased as SS particle size increased (Servizi and Martens 1987). Turbidity (light scattering) probably has no direct effect on lethal tolerance, but a sublethal response such as avoidance may be influenced by both turbidity and particle size. In order to facilitate comparison of research results, we recommend that investigators characterize the sediments which they study as to their particle size distribution and the relationship between SS and turbidity.

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A Fur Seal Simulation Model to Explore Alternative Management Strategies

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A simulation model is formulated for the South African fur seal (*Arctocephalus pusillus pusillus*) to evaluate the appropriate management action when culling to reduce population growth rate, culling to decrease fish consumption by seals, or harvesting to maximise numbers of seals removed. There is disturbance associated with bull sealing which increases pup mortality and reduces pregnancy rates, but this is not well quantified. Disturbance can be included or excluded from model runs. To reduce population growth, cow removal is most effective, but the population sex ratio becomes severely altered and this may be undesirable ecologically. Reduction of fish consumption is best achieved either by removing cows, with the same caveat regarding sex ratio, or by removing bulls and including disturbance effects. However, the acceptability of a reduction achieved by humans disrupting seals is questionable, and the continued removal of bulls may eventually lead to further decreases in pregnancy rate. To maximise a harvest, the relative commercial value of different seal products is considered, and bull removal, excluding disturbance effects, followed by removal of pups achieves this aim most effectively.

Les auteurs ont élaboré un modèle de simulation concernant l'otarie géante (*Arctocephalus pusillus pusillus*) afin d'évaluer la mesure de gestion appropriée lors de l'abattage sélectif en vue de réduire le taux de croissance démographique, l'abattage sélectif en vue de réduire la consommation de poisson par les otaries et la chasse en vue de maximiser le nombre d'otaries tuées. La perturbation qu'entraîne la chasse des mâles mène à une augmentation du taux de mortalité des jeunes otaries et à une baisse du taux de conception, mais cette perturbation n'a pas été adéquatement quantifiée. Elle peut être incluse dans les passages de modèle, ou en être exclue. Afin de réduire le taux de croissance démographique, il est plus efficace d'abattre des femelles bien que la proportion relative des sexes en est fortement modifiée; ceci peut ne pas être désirable au niveau écologique. Afin de réduire la consommation de poissons par les otaries, il est plus efficace d'abattre des femelles (et donc de modifier la proportion relative des sexes) ou des mâles (y compris la perturbation correspondante). On peut toutefois mettre en doute l'aspect acceptable d'une réduction des effectifs par l'entremise d'une chasse, source de perturbations; l'élimination continue de mâles peut éventuellement mener à de plus importantes baisses du taux de conception. Afin de maximiser le nombre d'otaries tuées, on tient compte de la valeur commerciale relative de différents produits de l'otarie; il est donc plus efficace d'abattre en premier lieu des mâles (à l'exclusion de la perturbation correspondante), puis des jeunes otaries.

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The recovery of seal populations in several marine systems following overexploitation and population declines in the eighteenth to mid-twentieth century has focussed attention on appropriate management measures, especially where seals are considered to affect commercial fisheries (e.g. Beverton 1985). Conservationists, responsible for acceleration of the recovery in recent years through lobbying to reduce commercial exploitation of seals, would like the population to remain unexploited whereas commercial sealers desire a maximum sustainable yield of seals. Some commercial fishermen, on the other hand, believe that seals eat too much fish and that these fish could otherwise be caught by the fishing industry. They would therefore like the seal population to be reduced to decrease the possible impact of seals on commercial fish yield, although to date, there is no evidence to suggest that reducing consumption of fish by seals will increase fishery yields (e.g. Butterworth et al. 1988; Anonymous 1991).

Resolving conflicting objectives is a complex management issue. Three important questions arise: what management action should we adopt in order to achieve efficiently (1) culling to reduce seal population growth rate, (2) culling to reduce fish consumption, and (3) harvesting to maximise number of seals removed over a period of time. In this paper, we develop a simulation model to provide insight into the case of the South African (Cape) fur seal (*Arctocephalus pusillus pusillus*) population. Because each of these three management objectives can be challenged by both scientific and ethical arguments, the aim here is not to justify the rationale behind each of them, but to provide an objective, even if theoretical, analysis of possible management action required to achieve differing future management scenarios with the use of simulation modelling. The benefit of using a modelling approach as opposed to empirical methods is that models create an ersatz world in which many trials, testing different management hypotheses, can be conducted in a short time without perturbing the system.

We draw the distinction between "culling," when the objective is to reduce the seal population efficiently, and "harvesting" in which seals are removed for the value of their products. We emphasise that action in which animals in one population are removed in order to provide benefit to another population is much less common in fisheries management than it is in the management of terrestrial systems.

Population Geography

Only one seal species, the South African fur seal, breeds off the west and south coasts of southern Africa, and the range of this population (Fig. 1) extends from northern Namibia (18°S) southwards as far as 34°S and along the south coast of South Africa as far as 26°E. There are 25 breeding colonies, 19 of which are on islands and the remaining six are mainland colonies. Ten known nonbreeding colonies were described by Oosthuizen and David (1988) and these are distinguished from breeding colonies by the absence of pups or minimal and erratic pup production. One of these colonies, Paternoster Rocks, has subsequently been classed as a breeding colony, bringing the total number of breeding colonies from 24 (David 1987) to 25. None of the colonies is located where human disturbance occurs. The island colonies are protected by their inaccessibility. Of the six mainland areas, five are in diamond-mining areas to which access is restricted and the remaining one, Cape Cross, is in a nature reserve. David (1989) suggested that Kleinsee and Atlas Bay are likely to be the largest mainland seal colonies in the world.

Following the near extirpation of the seals prior to 1900, numbers of pups have grown exponentially since 1972 at an average rate of 2.7% per annum (Butterworth and Wickens 1990). Breeding space does not appear to be a limiting factor at present, mainly because of access to extensive reasonably protected mainland breeding sites, particularly in Namibia. Food is more likely to be a factor that causes limitation to the population, but to date, this does not appear to have been a significant constraint to overall population growth, although pup numbers at some colonies have shown slowed growth in specific years (Wickens et al. 1991) and this can be attributed to food shortages. Bearing in mind that fluctuations in pup numbers do not necessarily mirror those of the population as a whole, population growth therefore appears to be density independent at present.

Life History

Bulls are polygynous and arrive at the colonies to set up territories from mid-October (Shaughnessy 1985), with the females arriving slightly later. The bulls are only present for the duration of the breeding season. Each territory consists of a small fixed area defended by a single bull, which may be visited by varying numbers of females. The females come and go at any time and are not tied to any particular territory. The pupping season lasts approximately 1 mo (Shaughnessy 1979; David 1987), with the median pupping date in early December (David 1987). Mating takes place, on average, 6 d after pupping (David and Rand 1986) and the gestation period is almost 1 yr, with delayed implantation of about 4 mo (Shaughnessy 1979). Each cow produces one pup which is fully weaned between the ages of 8 and 11 mo (David and Rand 1986; David 1987). The cows make regular feeding trips to sea alternating with visits to the colony to feed their pups, until the pups are weaned. Pups usually start foraging in the waters close to the colony at an age of 5–6 mo (David and Rand 1986). Outside the breeding season the animals that can be seen at a colony comprise the unweaned pups and their mothers, some juveniles of both sexes, and some other adults.

Sealing

During the present century, up to and including 1990, a total of 2 748 574 seals comprising 2 534 009 pups (92.2%), 205 009 bulls (7.5%), and 9556 cows (0.3%) have been killed (Wickens et al. 1991). Figure 2 shows the number of pups and bulls harvested since 1900. The number of pups killed increased dramatically from the 1930's and levelled off in the early 1970's. Since 1983, sealing has taken place mainly at the major mainland colonies, Cape Cross, Kleinsee, Wolf Bay, and Atlas Bay, and changes in the numbers of both pups and bulls harvested from these colonies are largely a consequence of changes in the market place as well as in management policy (Wickens et al. 1991).

Prior to 1983, the management policy for the South African fur seal was one of achieving a maximum sustainable yield of pups, the pelts of which were used in the fur trade. In 1983, a worldwide collapse in the market for furs caused a large drop in the trade of South African seal pup pelts, so sealing of pups was no longer as financially viable. Between 1984 and 1987, various actions were taken without the support of scientific advice to reduce the seal population with the objective of increasing the commercial fish yield, e.g. harvesting cows and increasing the harvest of bulls. Since 1988, quotas have been

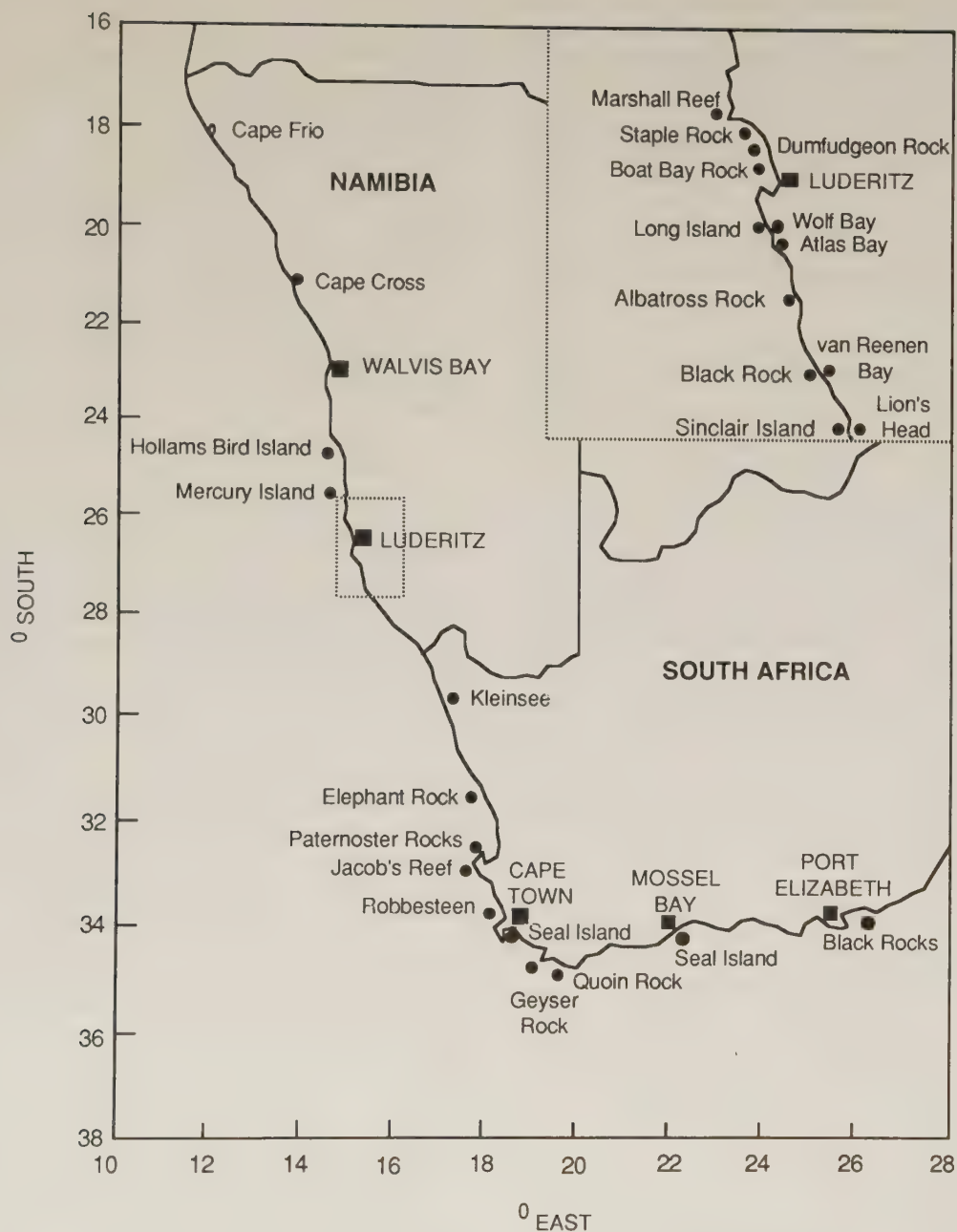


FIG. 1. Breeding colonies of the South African (Cape) fur seal (circles) throughout the extent of their range. The inset shows the colonies in the Luderitz area.

awarded according to scientific advice. The harvesting of bulls has increased in importance in recent years because the genitalia can be sold freely in the Far East. Pups are taken for their pelts which are marketed as leather goods or made into coats, and oil and meat are by-products from all seals harvested, although in recent years the by-products have not always been utilised.

The sealing seasons differ depending on which age or sex is being taken. Pups are generally taken from mid-July to mid-October, when they are approximately 8–11 mo old (weaning age), whereas the best time for removing adult bulls is in the first half of November, before the peak birth season. As a matter of experience, it is found that not only adult bulls are shot but also smaller bulls, some as young as about 6 yr old as judged from their body length. If a cow harvest is to be taken, then

the period causing least disruption to the population is late in the pup sealing season, from September to October, by which time there should be a minimal number of unweaned pups.

Associated with bull sealing is disturbance affecting cows with newborn pups and those about to pup. This phenomenon was noted decades ago (e.g. Rand 1955), but it has not been included in previous simulation models (e.g. Shaughnessy and Best 1980) presumably because of its indeterminate nature and its variability depending on the experience of the sealers and the timing of the harvest. If, due to poor management, bull sealing is allowed to extend into the peak pupping season, as has happened on some past occasions, then the consequences can include emigration of females and desertion of the pups by the cows, leading to death of these pups. This may lead to disruption of mating activities and hence reduced pup produc-

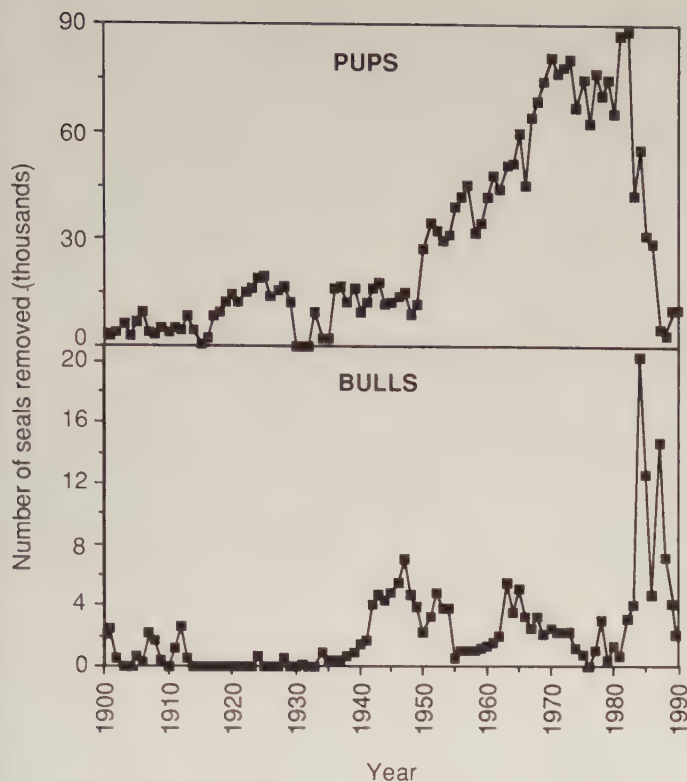


FIG. 2. Number of pups and bulls harvested since 1900 (data from Wickens et al. 1991). To date, cows have only been taken in 1985, 1988, and a few in 1989 and 1990.

tion at the colony the following year, both as a result of fewer pregnancies and the fact that some females do not return but move to another colony.

Model Structure and Parameterisation

The model is for a single, spatially unstructured population and is deterministic with a 1-yr time step, separate sexes, and partial age differentiation (ages 0–6+ yr). Population growth is density independent which is adequate for the purpose of the model, since there is no evidence of growth limitation, and defining a density-dependent function requires making too many assumptions for which there are no data. Options are included for sealing, disturbance effects of bull sealing, and estimation of food consumption. Natural mortality and mortality as a result of sealing operate independently.

It is only possible to examine the removals of certain individuals from the population for practical reasons involving the availability and selectivity of certain age and sex classes. The possible options are the killing of males (6 yr and older), breeding females, and pups (less than 1 yr old), all of which have been taken in the past from breeding colonies at particular times of year. Killing either nonbreeding females, most of which are between the ages of 1 and 5 yr, or males of the same age is not a practical management option because the sexes are not easily distinguished at this age. If seals of this age were to be taken, the two sexes would need to be taken together. This also presents problems in that these age classes are not concentrated at a colony during any particular period, so selection of these ages would be time-consuming, and this in turn would cause increased disturbance to the rest of the individuals on the colony. In the case of females, removing these individuals would be done as part of a culling programme, not as a harvest, since

females have virtually no financial value. As far as the males are concerned, the financial value of small males is less than that of older males because of the associated smaller mass of genitalia. Therefore, more of the smaller males would need to be killed to achieve the same harvested mass, and this requires a longer sealing season and greater processing time of the carcasses. For these reasons, both males and nonbreeding females aged between 1 and 5 yr are thought to be an inviable target for management consideration, and such removals have not been simulated.

Sealing rates of up to 60% are considered because these are the largest that are likely to be achievable in the field. Pregnancy rate is age dependent but assumed to be independent of bull abundance in the model. For this assumption there are no data, but since no sealing above a 60% rate is investigated, this is taken to be a robust assumption and the results viewed bearing this in mind. In the model, disturbance resulting from sealing operations at a colony causes an increase in pup mortality in the current year and a reduction in births in the subsequent year.

The model output is not scaled to true population size because the results required are merely to compare relative outcome under different management actions. The events occurring at a colony during one year (Fig. 3) are modelled by the following sequence of equations, and the data given in Table 1.

Sealing

Runs were carried out at a variety of sealing rates. Sealing rate is the number of seals removed relative to the number of pups born. This is done for reasons of practicality because it is only the pups that are censused and therefore only these can be used as a reference point, without making further assumptions about age structure being constant. The number of male and female pups (S_{m0} and S_{f0} , respectively) is reduced by the sealing rate of pups (C_p). The number of males in the last age class (S_{m6+}) is reduced by the number of bulls removed, which is the bull sealing rate (C_b) multiplied by the number of pups (S_0). The number of cows (S_{fi}) in each of the sexually mature (i.e. aged 3 yr and older) age classes is reduced by the number of cows removed, which is calculated as the cow sealing rate (C_c) times the number of pups times the percentage of females of that age divided by all sexually mature females. We have

$$\begin{aligned} S_{m0} &= S_{m0} (1 - C_p) \\ S_{f0} &= S_{f0} (1 - C_p) \\ S_{m6+} &= S_{m6+} - (C_b * S_0) \\ S_{fi} &= S_{fi} - (C_c * S_0 * S_{fi} / \sum_{j=3}^6 S_{fj}) \quad \text{for } i \geq 3. \end{aligned}$$

Survival

The number of males that are territorial (S_t) is calculated by dividing the number of sexually mature cows (aged 3 yr and over) by the female aggregation size (A). In order to account for the mortality of territorial males (M_t), the mortality rate of the males in age class 6+ (M_{m6+}) is estimated by apportioning territorial mortality and older natural mortality (M_a) to the number of territorial males and other males aged 6 and older (S_{m6+}), respectively. We have

$$\begin{aligned} S_t &= \sum_{i=3}^6 (S_{fi}) / A \\ M_{m6+} &= ((S_{m6+} - S_t) (1 - M_a) + S_t (1 - M_t)) / S_{m6+}. \end{aligned}$$

TABLE 1. Parameter values for the model. The notation presented here is subscripted by "m" for males, "f" for females, and "l" for lactating females in the model equations. See text for details on source of data for parameter values.

Parameter	Notation	Males	Females	Lactating females	Source(s)
Annual pregnancy rate (%)					
3 yr old	P_3	—	41	—	Butterworth and Wickens 1990
4 yr old	P_4	—	66	—	Butterworth and Wickens 1990
5+ yr old	P_{5+}	—	83	—	Butterworth and Wickens 1990
Annual mortality rate (%)					
Pups	M_0	25	25	—	de Villiers and Roux 1992
Juveniles and adults	M_a	12	12	—	Butterworth 1990
Territorial bulls	M_t	29	—	—	Butterworth 1990
Average mass (kg)					
1 yr old	W_1	25	21	—	Butterworth and Wickens 1990
2 yr old	W_2	34	28	—	Butterworth and Wickens 1990
3 yr old	W_3	43	35	—	Butterworth and Wickens 1990
4 yr old	W_4	54	42	—	Butterworth and Wickens 1990
5 yr old	W_5	62	49	—	Butterworth and Wickens 1990
6+ yr old	W_{6+}	140	60	—	Butterworth and Wickens 1990
Percentage body mass consumed daily					
1 yr old	R_1	6.5	6.7	—	Innes et al. 1987
2 yr old	R_2	6.1	6.3	—	Innes et al. 1987
3 yr old	R_3	5.8 ^a	5.6 ^a	10.0 ^b	^a Innes et al. 1987;
4 yr old	R_4	5.5 ^a	5.9 ^a	10.0 ^b	^b SFRI, unpubl. data
5 yr old	R_5	5.4 ^a	5.7 ^a	10.0 ^b	
6+ yr old	R_{6+}	4.6 ^a	5.4 ^a	10.0 ^b	
Percentage of males at weaning	B_m	57	—	—	Oosthuizen 1991
Percentage of year from birth to weaning	T	79	79	—	David and Rand 1986; David 1987
Number of cows in an aggregation	A	—	28	—	Rand 1967
Disturbance					
Culling rate at maximum disturbance					
Current year	CD_1	15	15	—	Assumed
Subsequent year	CD_2	20	20	—	Assumed
Loss in pup production (%)					
Current year	MD_1	15	15	—	Assumed
Subsequent year	MD_2	50	50	—	Assumed
Starting number of pups (millions)	S_0	0.5	0.5	—	—

The number of seals of each age and sex (S_i) grows into the next age class, once it has been reduced by natural mortality (M). The number of seals in age class 6+ includes those already in age class 6+ and the seals moving up from age class 5. In the case of pups, the number of 1-yr-olds of each sex is calculated by applying the observed sex ratio (B_m). We have

$$\begin{aligned}
 S_{m6+} &= (S_{m5} + (S_{m6+} (1 - M_{m6+}))) \\
 S_{f6+} &= (S_{f5+} + (S_{f6+} (1 - M_a))) \\
 S_i &= S_{(i-1)} (1 - M_{(i-1)}) \quad \text{for } i = 2 \text{ to } 5 \\
 S_{m1} &= S_{m0} (1 - M_0) B_m \\
 S_{f1} &= S_{f0} (1 - M_0) (1 - B_m).
 \end{aligned}$$

One mortality rate is used for pups for the range of values given in de Villiers and Roux (1992), so the number of pups of each sex is calculated by altering the sex ratio to that observed, which is skewed towards females (Oosthuizen 1991). Mortality rates for older seals are derived from the distribution of known-age females collected at sea for research, and mor-

tality rate for territorial bulls is calculated from resightings of branded animals (Butterworth 1990). The size of an average female aggregation used as input into the model is estimated from data on counts of all females and territorial bulls in different areas of a colony (Rand 1967).

Disturbance

In the absence of appropriate field data, piecewise-linear disturbance functions for the current (D_1) and subsequent year (D_2) are assumed, dependent on the sealing rate of bulls (C_b) (Fig. 4). Maximum disturbance is denoted by MD_1 for the current year and MD_2 for the subsequent year. CD_1 and CD_2 are the sealing rates above which disturbance is assumed to be constant for the current and subsequent years, respectively. If there is disturbance from the previous year and during the current year, their effects are multiplied.

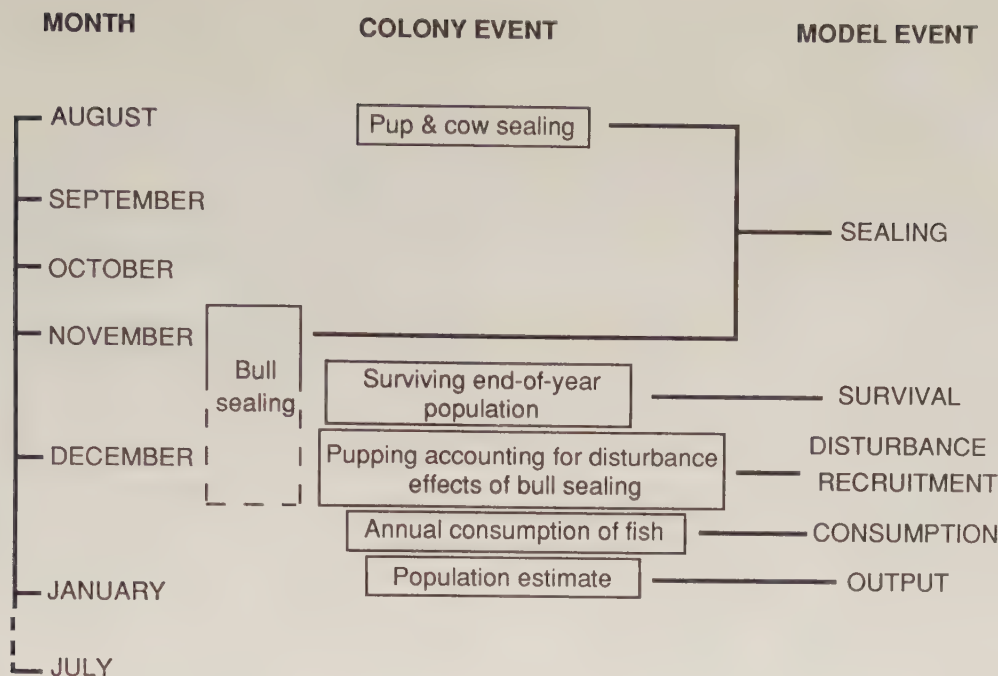


FIG. 3. Temporal sequence of events at a colony and the corresponding sequence in the simulation model.

If $C_b > CD_1$ then if $D_1 = 0$ then $D_1 = CD_1$
 else $D_1 = 1 - (1 - D_1)(1 - MD_1)$
 else if $D_1 = 0$ then $D_1 = C_b$
 else $D_1 = 1 - (1 - D_1)(1 - C_b)$
 If $C_b < CD_2$ then $D_2 = (MD_2/CD_2) C_b$
 else $D_2 = MD_2$.

Assumptions about bull sealing disturbance are based on observations of the disturbance caused by large bull harvests at Kleinsee. In 1984, 10 035 bulls were taken, followed by 6223 bulls and 6890 cows in 1985 (Wickens et al. 1991). Mortality of pups appears to have increased in the years of the large bull harvests because sealing extended right into the peak pupping season (Best 1990). Aerial surveys showed a decrease from 83 469 pups at the end of 1983 down to 43 267 and 47 113 at the end of 1985 and 1986, respectively. The removal of cows in 1985 would immediately reduce the number of births by approximately 7000 that year, but the decreased pup production is also attributed to reduced number of pregnancies resulting from disturbance during 1984 and, possibly, emigration from the colony. The sealing rate of bulls in 1984 can be calculated as 12% of the number of pups born at the end of 1983. For the purpose of the model, it is assumed that above particular sealing rates, the amount of disturbance remains constant whereas below them, it decreases linearly. These disturbance effects can be included or excluded from the model so that the consequences thereof can be evaluated.

Recruitment

Each cow produces only one pup, so the number of pups (S_0) is estimated by the sum of the number of females (S_i) that are pregnant (P_i) multiplied by the proportion of pups that are either not born (because of lowered pregnancy rates) or die as a result of disturbance (D_1):

$$S_0 = \sum_{i=3}^6 (P_i S_{fi}) (1 - D_1).$$

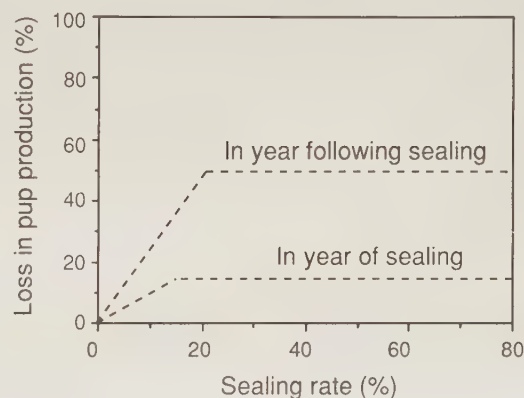


FIG. 4. Functions describing the effect of disturbance during bull sealing operations on pup production, as assumed in the model.

Age-specific pregnancy rates are estimated from the number of pregnant females in samples of seals collected for research purposes (modified from Butterworth and Wickens 1990).

Consumption

In the i th age class, males (S_{mi}), lactating cows (L_i), and nonlactating cows ($S_{fi} - L_i$) consume different amounts and are therefore treated separately. Cows with pups are assumed to be lactating for a portion of the birth year (T) which is taken as 9.5 mo, based on the information from David and Rand (1986) and David (1987). The total amount of fish consumed (F) is calculated by the following set of equations:

$$L_i = \sum_{i=3}^6 [P_i S_{fi} (1 - D_1) T]$$

$$F = \sum_{i=3}^6 [(S_{mi} W_{mi} R_{mi}) + (L_i W_{fi} R_{fi}) + ((S_{fi} - L_i) W_{fi} R_{fi})]$$

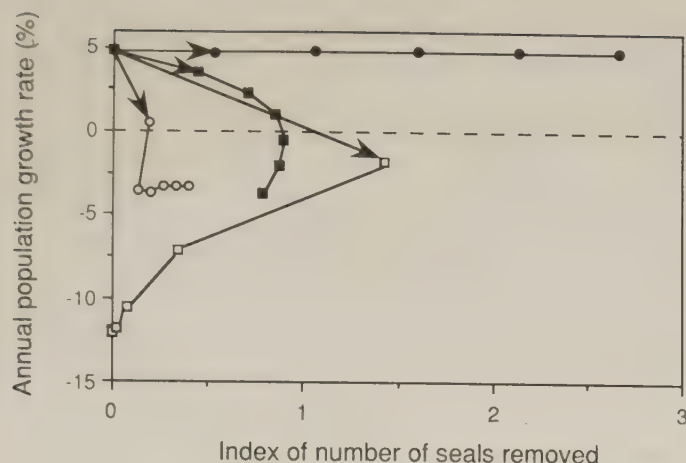


FIG. 5. Annual growth rate after 20 yr as a function of an index of the number of seals removed as simulated by the model under different management schemes. The cull rate increases in steps of 10% between 0 and 60% in the direction of the arrows for the culling of pups (solid squares), cows (open squares), bulls excluding disturbance effects (solid circles), and bulls including disturbance effects (open circles).

where W_{mi} and W_{fi} are, respectively, the mean mass of a male seal and female seal of age i and R_{mi} , R_{li} , and R_{fi} are, respectively, the annual percentage of body mass consumed by males, lactating females, and nonlactating females. Age-specific body mass values are estimated from seals collected at sea for research (Butterworth and Wickens 1990) with the figure for 6+-yr-olds calculated as the masses of ages 6 yr and older weighted by a population age distribution (SFRI, unpubl. data). The mass-specific consumption rates for males and nonlactating females are calculated using the biomass ingestion equation in Innes et al. (1987) for marine mammals, and for lactating females, a rate is assumed (SFRI, unpubl. data).

Model Results

The control of seal population growth rate, reduction in fish consumption, and maximising of number of seals harvested were explored by simulating the sealing of pups, bulls, and cows separately at rates between 0 and 60%. Values are output from the model at the time when the model population is maximum, i.e. directly after recruitment. Outcomes of the different scenarios are compared after 20 yr of simulation because, with the given model structure, a stable age distribution is achieved after approximately this time period. The model is not scaled to true population size; therefore, the number of seals removed and the amount of fish consumed is a relative scale and is an index of the number removed and consumption. The efficiency of each scenario is compared. In this context, for the objective variables of population growth rate and seal consumption of fish, efficiency is defined as the largest change in each of these with small increase in sealing rate (cull or harvest) after 20 yr. In the case of the objective variable, harvest size, efficiency is merely the greatest number that can be removed even after 20 yr.

Culling to Reduce Population Growth Rate

Under a regime without culling, the annual population growth rate of the model population is 4.8% (Fig. 5). Based on census data (Wickens et al. 1991), the annual growth rate of pups at colonies that have undergone no sealing through the census period is in the region of 3%. In the past few decades, pup

numbers of the South African fur seal population have averaged an annual growth rate of 2.7% (Butterworth and Wickens 1990). Historically, mainly pups and bulls have been removed from the population at highly variable rates, the rate of pup removal having ranged between 45 and 1%, averaging 26%, and that of the bulls between 0 and 8%, averaging 2%, in the last two decades (Wickens et al. 1991). The model shows that under the average historical pup sealing rate, the annual population growth rate is 1.7%, while that under the historical bull sealing rate is between 3.9 and 4.8%, depending on whether disturbance effects are included or not. It must be remembered that the growth rate will have varied annually, depending on the combination of sealing rates. In addition, the model results in Fig. 5 show population growth rate whereas that measured from census data is the growth rate of the pups only, which, because of the history of sealing, are not necessarily exactly the same. The growth rates are sufficiently similar to that estimated by Butterworth and Wickens (1990) and from the data in Wickens et al. (1991) to demonstrate that the model output adequately reflects the growth rates found in nature.

As expected, population growth rate drops off with the number of seals removed under any of the scenarios (Fig. 5). However, for pup and cow culls, the number of seals required to be removed to obtain further decreases in population growth declines above a certain cull rate because the population has been reduced after 20 yr and there are fewer seals from which removals can be made. In the cases of pup culling and of bull culling including disturbance effects, the results shown after 20 yr may differ from those after a shorter period because of the time lag between the decrease in number of pups and the time to maturity of females (~5 yr) when overall pup production will be reduced.

Considering first the case with disturbance effects of bull culling excluded, removing bulls causes little decrease in annual growth rate because an assumption of the model is that pregnancy rate is independent of the number of bulls. At larger culling rates (>10%) the removal of cows is most efficient in reducing population growth rate. At a low culling rate of cows, a negative population growth rate can be achieved but slightly less efficiently than when pups are being removed, but a larger culling rate of pups is required to achieve this.

If there is disturbance resulting from the culling of bulls, then the removal of bulls may be more efficient than the removal of cows at low cull rates. At bull cull rates above 20% the effects of disturbance are assumed constant, and therefore, with additional removals, the population growth rate is not reduced any further. At high cull rates of cows, greater reduction in population growth rate is achievable.

Three features associated with cow and bull culling need to be considered. Firstly, when cows are being heavily culled, the model shows that the sex ratio becomes strongly skewed towards males, and at a 60% cull rate, the population becomes almost entirely male (Fig. 6). Such altered sex ratios have not been observed in nature and many have unforeseen consequences with respect to social structure of the population, and these are not accounted for in the model. Secondly, a long-term undesirable consequence of culling bulls may result from the continued removal of the largest bulls, which will be replaced by smaller bulls. These smaller bulls, being territorial and therefore having to spend a large amount of time on the colony without food, might not have adequate fat reserves and would therefore suffer even greater mortality than that already affecting large territorial bulls. A consequence of this might also be reduced pregnancy rates, if many of the small bulls die early

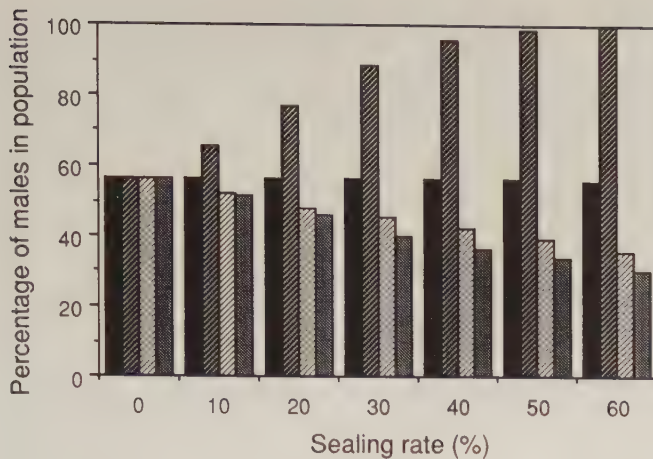


FIG. 6. Percentage of males in the population after 20 yr as a function of the cull rate of seals as simulated by the model under different management schemes, which include the culling of pups (solid), cows (dark hatch), bulls excluding disturbance effects (light hatch), and bulls including disturbance effects (stippled).

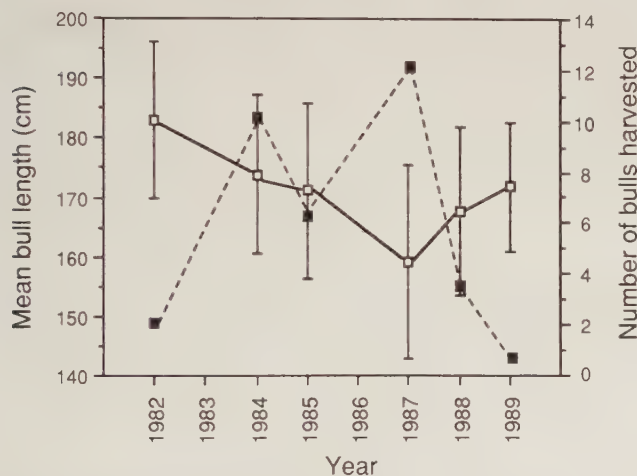


FIG. 7. Change in the length of bulls taken (open squares) in the harvest at Kleinsee (SFRI, unpubl. data) and the number of bulls harvested (solid squares) (Wickens et al. 1991) since bull sealing began there in 1982.

in the breeding season. The mean size of bulls harvested at Kleinsee (SFRI, unpubl. data) decreased during the 1980's (Fig. 7) because smaller bulls were taken to fill the large quotas during this time. In 1988 and 1989 the size of bulls in the harvest increased, but this was because the small harvest allowed remaining larger bulls to be taken preferentially. Thirdly, the killing of pregnant cows (unavoidable because of the 12-mo gestation period) and of bulls when there is associated disturbance causing pup mortality may be considered to be undesirable on grounds of cruelty.

Culling to Reduce Fish Consumption by Seals

Simulations of the reduction in seal consumption of fish through the removal of seals give a similar result to that obtained when the objective was reducing the population growth rate (Fig. 8). The major difference is that when bulls are culled, fish consumption decreases whereas in terms of population growth rate in numbers, there is virtually no decline. This results from heavier bulls eating a much larger amount of fish per capita than other seals. Culling either pups or cows will achieve a

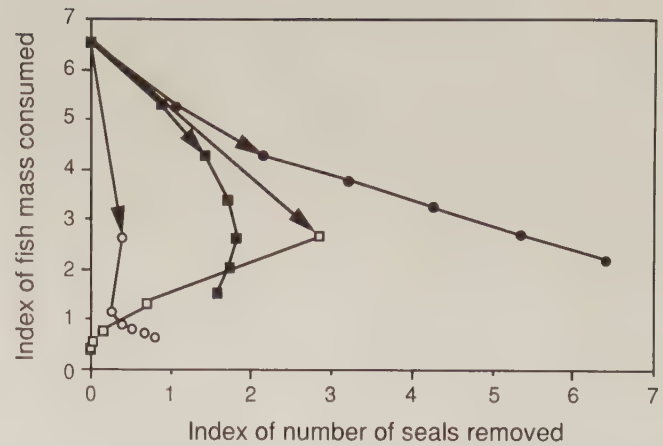


FIG. 8. Amount of fish consumed by the seal population after 20 yr as a function of an index of the number of seals removed as simulated by the model under different management schemes, both excluding and including the disturbance associated with bull culling. The cull rate increases in steps of 10% between 0 and 60% in the direction of the arrows for the culling of pups (solid squares), cows (open squares), bulls excluding disturbance effects (solid circles), and bulls including disturbance effects (open circles).

large reduction in fish consumption, but the culling of cows is much more efficient and results in a greater population reduction above a 10% cull rate. If disturbance during bull removals is assumed in the model, then culling bulls can achieve almost the same reduction in consumption as culling pups or cows, and it is similarly efficient.

Harvesting to Maximise Seal Removals

The results obtained from the culling simulations can also be used to compare the numbers obtained from pup, cow, and bull harvests (see Fig. 5). Assuming no disturbance resulting from bull removals, the largest number of animals removed at a set population growth rate can be achieved by harvesting bulls. If there is disturbance resulting from bull removals, then, for a set population growth rate, at low harvest rates (~10%), more cows than pups or bulls may be harvested. At other harvest rates, the largest harvest of seals may be achieved by taking pups.

Sensitivity Analysis of Outcomes under Management Actions

The results of a 10% increase in pregnancy, survival, and consumption rates from their values in Table 1 on a single run (i.e. changes which lead to enhanced population size and greater consumption) and likewise to a 10% decrease in these parameter values (i.e. changes which lead to decreased population size and lower consumption) alter some of the conclusions reached above (Fig. 9).

If the parameters are altered so that pup production is enhanced, the difference is basically that culling cows causes the largest decrease in population growth rate and consumption and this is done most efficiently. If parameter conditions are changed to lead to decreases in overall pup production, the same pattern emerges. This results because by increasing survival and fecundity, the breeders in the population are most affected and therefore, when reduced in number, most affect the population. The model population is not scaled to true population size, so annual population growth simply moves up or down the scale when parameter values are altered. No difference is

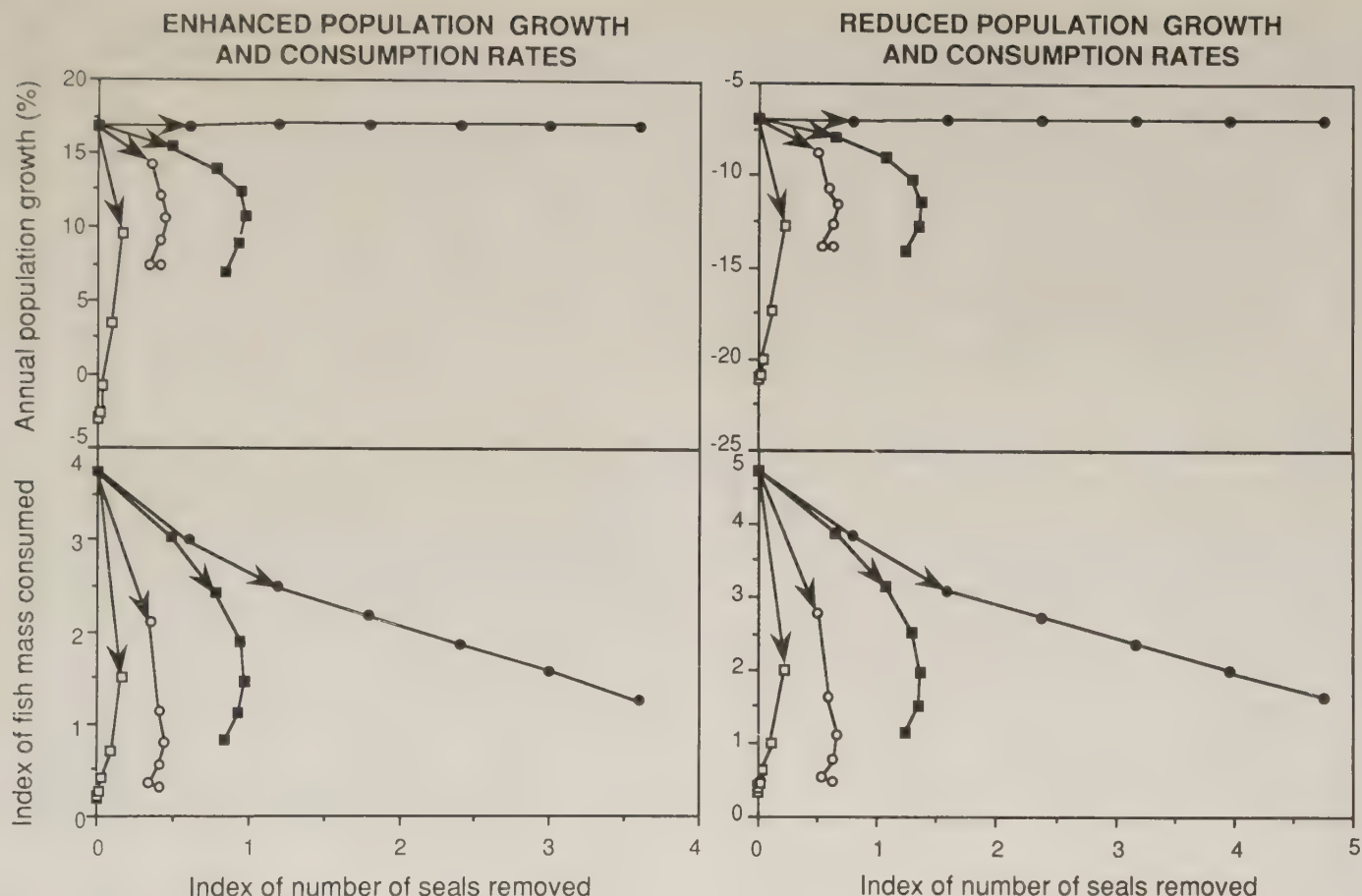


FIG. 9. Sensitivity analysis of annual population growth and amount of fish consumed by the seal population after 20 yr as a function of an index of the number of seals removed. These are simulated by the model under different management schemes when parameter values are altered to either enhance population growth and consumption rates or to reduce growth and consumption. The sealing rate increases in steps of 10% between 0 and 60% in the direction of the arrows for the culling of pups (solid squares), cows (open squares), bulls excluding disturbance effects (solid circles), and bulls including disturbance effects (open circles).

detectable in the percentage of males in the population under the different conditions of the sensitivity analysis (not shown).

Comparison of Effectiveness of Management Actions

The simulations suggest that, under the model assumptions, and accounting for the results of the sensitivity analysis, different strategies should be adopted for managing the seal pop-

ulation depending on whether the objective is to reduce seal population growth rate, reduce fish consumption, or maximise the seal harvest. The effectiveness of the management actions relative to the three objectives is summarised in Table 2, based on the management actions that are considered feasible and practical. Effectiveness is measured by combining the success with which the management action achieves the desired result and the efficiency with which it is achieved. In the case of

TABLE 2. Summary of model results with respect to the three management objectives and alternative management actions.

Management action	Management objective									
	Reduce population growth rate			Reduce fish consumption			Maximise seal harvest			
	Success level (S)	Effectiveness Efficiency (E)	(rating based on S and E)	Success level (S)	Effectiveness Efficiency (E)	(rating based on S and E)	Success level (S)	Effectiveness Efficiency (E)	Economic value (V)	Effectiveness (rating based on S, E, and V)
Pup removal	Medium	Medium	3	High	Medium	3	Medium	Medium	Medium	2
Cow removal ^a	High	High	1	High	High	1	Low	Low	Low	4
Bull removal ^b with no disturbance	Low	Low	4	Low	Low	4	High	High	High	1
Bull removal ^b with disturbance ^c	Medium	High	2	High	High	1	Low	Low	High	3

^aBut sex ratio severely altered — Desirable?

^bBut continued removal of bulls causes reduced pup production — Desirable?

^cBut pup mortality increased because of disturbance — Acceptable?

maximising a harvest, the effectiveness is further weighted by an index of the relative economic value of the products. Specific economic values for each of the seal products are difficult to obtain, particularly as they vary depending on the political climate of the time and the acceptability of their sale (Wickens et al. 1991). Therefore, an index of their importance commercially is most appropriate and is indicated in Table 2 as being indicative of the situation at the present time. Management actions are ranked according to their effectiveness.

If there were no disturbance during bull removals, then the most effective strategy for achieving either a reduction in seal population growth rate or reduced fish consumption is the removal of cows. However, the severe skewing of the sex ratio under a cow culling regime may be ecologically undesirable and could lead to destabilisation or extinction. If the objective is to maximise the number of seals taken, then the removal of bulls is most effective. The effectiveness of a pup harvest is secondary to that of bulls, both in terms of the number taken and the economic value of the products. Not only is the removal of cows ineffective in terms of numbers removed, cows also currently have a low per capita economic value, and therefore the removal of cows is clearly a poor choice with respect to maximising harvest.

If there is disturbance during bull removals, then the most effective action for obtaining a reduction in fish consumption may be the removal of bulls, and this action may also be quite effective in reducing seal population growth rate. However, the reduction is caused partly by increased mortality of pups which is not an acceptable means because it permits deliberately poor management, and it may not be desirable to remove large bulls continually.

Two of the management goals, achieving a reduced growth rate of the seal population and reducing fish consumption by the population, are compatible whereas the remaining goal, achieving the most profitable harvest from the seal population, is not compatible with the first two. Since management policy is likely to attempt to account for some combination of these three goals, this may best be achieved, not by removing one sex or age class exclusively, but by removing animals from a combination of sex and age classes, the proportions varying depending on the relative weight assigned to the three goals.

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A Bioenergetics Model of Zebra Mussel, *Dreissena polymorpha*, Growth in the Great Lakes

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Schneider, D. W. 1992. A bioenergetics model of zebra mussel, *Dreissena polymorpha*, growth in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 49: 1406–1416.

An individual growth model of the zebra mussel, *Dreissena polymorpha*, is presented, based on weight- and temperature-specific physiological parameters taken from the literature on zebra mussels and marine mussels. Given food availability and water temperature the model can predict growth and consumption of zebra mussels in diverse environments. The model was tested with data from Lake Constance and matches observed growth fairly closely. Using the functional response of zebra mussels to increasing food concentration, the model simulates individual zebra mussel growth in novel habitats. For the Great Lakes, the following predictions were made: zebra mussels have bimodal growth patterns, with rapid growth in the spring and fall during periods of high food availability and moderate temperatures; growth rates are highest in Lake Ontario and lowest in Lake Superior, reflecting the trophic gradient in the Great Lakes; based on published weight/fecundity relationships, zebra mussels reach reproductive size in all of the Great Lakes except the main body of Lake Superior; and local eutrophication (e.g. Duluth/Superior Harbor) increases zebra mussel growth rates. Modelled consumption rates in Lakes Erie and Ontario are also consistent with rates of consumption by the zebra mussel in eutrophic and mesotrophic European lakes.

L'auteur présente un modèle de croissance de la moule zébrée, *Dreissena polymorpha*, basé sur des paramètres physiologiques liés au poids et à la température relevés dans des ouvrages publiés sur la moule zébrée et des moules marines. Si l'on inclut la disponibilité de nourriture et la température de l'eau dans le modèle, il permet de prédire le taux de croissance et le taux de consommation chez des moules zébrées peuplant divers milieux. Le modèle, vérifié à l'aide de données recueillies dans le lac Constance, correspondait assez étroitement au taux de croissance observé. En utilisant la réaction fonctionnelle de la moule zébrée à des concentrations croissantes de nourriture, le modèle simule la croissance de chaque moule dans un nouvel habitat. Dans le cas des Grands Lacs, l'auteur a formulé les prévisions suivantes: un régime de croissance bimodal, soit une croissance rapide au printemps et à l'automne lorsque la nourriture est abondante et que la température de l'eau est modérée; un taux de croissance plus élevé dans le lac Ontario et plus faible dans le lac Supérieur à cause du gradient trophique des Grands Lacs; d'après les relations entre le poids et la fécondité relevées dans des ouvrages publiés, la réalisation de la taille de reproduction dans tous les Grands Lacs, sauf dans le bassin principal du lac Supérieur; et la stimulation de la croissance entraînée par l'eutrophisation au niveau local (par ex., le port de Duluth/lac Supérieur). Les modèles des taux de consommation dans les lacs Érié et Ontario concordent aussi aux taux de consommation montrés par la moule zébrée de lacs européens mésotrophes et eutrophes.

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The Laurentian Great Lakes have been subject to the invasion of a large number of exotic species. The success of the invading species and their effects on the Great Lakes ecosystem have varied. Some have remained rare and had little effect, while others, such as the alewife (*Alosa pseudoharengus*) and sea lamprey (*Petromyzon marinus*), have had enormous biological and economic impact. A recent invader, the zebra mussel, *Dreissena polymorpha* (Pallas), was first found in the Laurentian Great Lakes in 1988, in Lake St. Clair, Ontario (Hebert et al. 1989). The zebra mussel has a great dispersal capacity through its pelagic larvae and ability to attach to vessels and has now reached all of the Great Lakes (New York Zebra Mussel Information Clearinghouse 1990). Zebra

mussels have reached very high densities in Lake Erie and are increasing in Lake Ontario, but their potential population growth rate in other Great Lakes is not known. In addition, the effects of zebra mussels on food web dynamics, sedimentation, and contaminant cycling are unknown.

Predictive models offer a method for assessing the potential impact of zebra mussels on the Great Lakes and other lake ecosystems. One critical question, important in evaluating the potential impact of zebra mussels ecosystems, is in which lakes will zebra mussel populations reach nuisance levels?

To answer this question, I developed a bioenergetic model which simulates individual zebra mussel growth as a function of temperature, mussel size, and phytoplankton concentration. Models of individual growth rates combined with the weight-dependent fecundity relation for zebra mussels can be used to estimate population growth rates. Unless otherwise noted, however, growth rates here refer to individual weight increases. In

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this paper, I describe the model, test it using growth rate data from European lakes, and apply it to some questions concerning the role of zebra mussels in North American lakes.

The Model

The bioenergetics model for *Dreissena* follows those developed for fish and other organisms with indeterminate growth by Kitchell et al. (1977) and others. The general approach of these models is described in Adams and Breck (1990) and Wootton (1990). Briefly restated, the model is used to balance an energy budget when one of the terms is used as an unknown. In most cases, the unknown is the rate of growth or food consumption. All of the simulations described in this paper were run using a computer program developed by Hewett and Johnson (1987, 1989) and available from the University of Wisconsin Sea Grant Institute (1800 University Avenue, Madison, WI 53705, USA). A version of the model for largemouth bass (*Micropterus salmoides*) was tested against field measurements and successfully modelled the seasonal patterns of growth in this species (Rice and Cochran 1984).

The model uses a balanced energy budget approach to simulate zebra mussel bioenergetics. The parameter units are in terms most often measured: oxygen for respiration and grams for consumption. Calculations are made in terms of energy and converted to appropriate weights such that net energy gains or losses are balanced by equivalent weight changes:

$$(1) \quad dW/dt = C - (R + F + U + G)$$

where W is weight, t is time, gains are consumption (C), and losses are respiration (R), egestion (F), excretion (U), and reproduction (G). The model calculates the terms of this budget on a daily basis, providing estimates of individual growth rates, consumption, or population production over the simulation period.

Gains and losses are calculated according to temperature- and weight-dependent rates. Estimates for these parameters were taken from the physiological literature on zebra mussels, as well as marine mussels where zebra mussel data were unavailable. The parameter symbols and values are summarized in Table 1. Below, I describe in more detail the parameterization of the model, especially where it differs from past applications.

Respiration

In zebra mussels, as in most suspension feeding bivalves, the gills are the site of both gas exchange and the trapping of food particles in mucus secretions. For this reason, consumption rate and respiration rate are not independent, and respiration is dependent on ration, the quantity of food consumed. Under conditions of starvation, or zero ration, pumping rates, and thus respiration rates, are typically low and are described by a "standard" metabolic rate (Bayne and Newell 1983). As food level increases, pumping rate increases, and with it, respiration, which can now be described by an "active" rate. Following a pulse in food availability, filtering rate declines from the peak active rate to a "routine" rate, intermediate between the standard and active rates. Any model of zebra mussel respiration has to account for these rates which are dependent on the ration.

Standard respiration rate (R) is modelled as a function of the weight of the mussel and water temperature:

$$(2) \quad R = a_r W^{b_r} f(t)$$

where W is the wet weight of the soft body of the mussel in grams, a_r is the standard respiration rate of a 1-g zebra mussel at the optimal temperature for respiration in grams of oxygen per gram of mussel per day, b_r is the exponent for the weight dependence of respiration, and $f(t)$ is a multiplier ranging from 0 to 1 for the temperature dependence of respiration, described by a temperature-dependence function from Kitchell et al. (1977), and fit to data of Woynarovich (1961) for zebra mussels (Fig. 1). Respiration rates are converted to calories using an oxycaloric coefficient of $3240 \text{ cal} \cdot \text{g O}_2^{-1}$ (Stewart et al. 1983) and to grams of body mass using the caloric density of the zebra mussel (Table 2). This respiration rate – temperature curve shows little evidence of acclimation. Typically, marine mussels do not exhibit acclimation in the standard metabolic rate (Bayne et al. 1973); their respiration rates do not decrease following exposure to higher temperatures. However, the routine and active rates, which are reflected in consumption rates, may show some acclimation.

There are no reliable data for the relationship between body weight and respiration of zebra mussels. Values in the literature for b_r range from -0.33 to 0.05 (Walz 1978c). Bayne and Newell (1983) suggested that the slope for marine filter-feeding bivalves typically varies from -0.33 to -0.25 , with a mean over a large number of organisms and temperatures of -0.273 . I used -0.25 in the model, following Walz (1978c).

To estimate a_r , the specific respiration rate for a 1-g zebra mussel at the temperature for optimal respiration, I used data reported by Walz (1979) in which the weight loss of unfed zebra mussels was measured over 25 d at 20°C . Respiration under these conditions may better reflect the true standard metabolic rate than short-term laboratory experiments which measure respiration directly. I then ran the model at various values of a_r , until weight loss in the model matched observed weight loss for zebra mussels. While the data were not reported for a 1-g zebra mussel at the optimal temperature, the temperature-dependence and weight-dependence functions in the model scaled a_r to the appropriate size and temperature.

In suspension feeders, metabolic activity increases greatly with filtration or feeding activity (Bayne et al. 1976). This is reflected in higher routine and active metabolic rates. The energetic cost of feeding can be broken down into two processes: the mechanical cost of water transport and the specific dynamic action (SDA; the physiological cost of digestive processes including deamination). Bayne and Scullard (1977) have estimated the mechanical cost of feeding as 47% and SDA as 8% of consumption for *Mytilus edulis*. This represents the maximum increased cost of feeding, realized during active metabolism. Under most feeding conditions, mussels will respire at a lower, routine rate and the cost of feeding will be substantially less (Bayne and Scullard 1977; Griffiths and Griffiths 1987). I have used an arbitrary value of 28.5% for the combined mechanical and physiological costs of feeding and digestion (called SDA in Table 2), intermediate between no cost of feeding and the cost as determined by Bayne and Scullard (1977) for active metabolism.

Consumption

Consumption (C) is modelled as a function of weight, temperature, and food availability:

$$(3) \quad C = a_c W^{b_c} f(t) \cdot P\text{-value}$$

where a_c is the maximum consumption rate of a 1-g zebra mussel at the optimal temperature for consumption in grams per gram per day, b_c is the exponent for the weight dependence of

TABLE 1. Symbols and parameters used in model equations of zebra mussel growth.

Symbol	Parameter description	Parameter value
<i>Consumption</i>		
a_c	Intercept for maximum consumption ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)	0.031
b_c	Exponent for maximum consumption	-0.39
Q	Lower temperature at which consumption is k_1 maximum	2°C
T_0	Lower temperature at which consumption is 0.98 maximum	12°C
T_m	Higher temperature at which consumption is 0.98 maximum	21°C
T_l	Higher temperature at which consumption is k_4 maximum	32°C
k_1	Empirical coefficient for Q	0.1
k_4	Empirical coefficient for T_l	0.02
<i>Respiration</i>		
a_r	Intercept for maximum standard respiration ($\text{g O}_2 \cdot \text{d}^{-1}$)	0.003
b_r	Exponent for maximum standard respiration	-0.25
Q	Temperature dependence of respiration (Q_{10})	3.1
T_0	Optimum temperature for standard respiration	28°C
T_m	Maximum temperature for standard respiration (= upper lethal)	31°C
SDA	Specific dynamic action + energetic cost of feeding	0.285
<i>Egestion/excretion</i>		
α_f	Intercept of proportion of consumed food egested	0.315
γ_f	Coefficient for feeding level dependence of egestion	0.88
α_u	Proportion of consumed food excreted	0.064

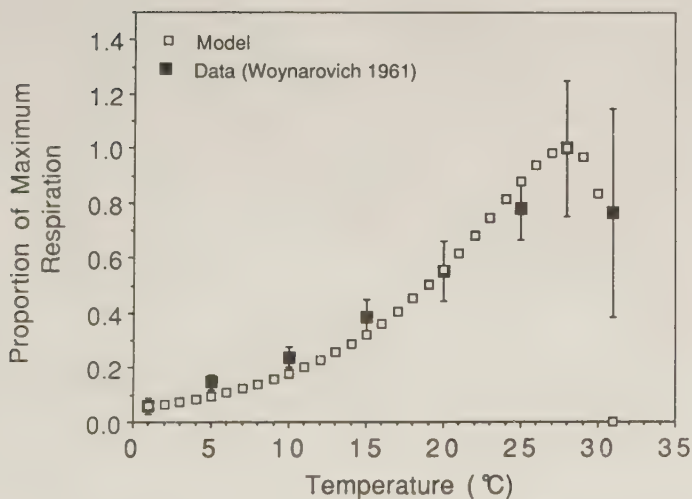


FIG. 1. Respiration, as a proportion of maximum, versus temperature, as reported in Woynarovich (1961) ± 1 SD, and as modelled. Model points are from the temperature-dependence function described by Kitchell et al. (1977) with parameters from Table 1.

consumption, W is the wet weight of the soft body of the mussel in grams, and $f(t)$ and P -value are multipliers ranging from 0 to 1 for the temperature dependence of respiration and the proportion of maximum consumption realized, respectively. An important aspect of this model is that consumption reflects the amount of material ingested, rather than the amount of material filtered. Thus the amount of filtered material which is rejected as pseudofeces is not included in rate of consumption.

The temperature dependence for consumption was taken from Walz (1978a) and Reeders and Bij de Vaate (1990) for zebra mussels. Walz (1978a) suggested a maximum consumption at 12.5°, steeply dropping below 8°C and above 15°C. Reeders and Bij de Vaate (1990), however, suggested a response with

TABLE 2. Factors used to convert various estimates of zebra mussel and algae weight and caloric values to uniform units used in the bioenergetics model.

<i>Mussels</i>	
Dry weight	$= 0.15 \cdot \text{wet weight}^a$
Carbon content (mg)	$= 0.45 \cdot \text{dry weight (mg)}^b$
Wet weight (mg)	$= 0.071 \text{ length (mm)}^{2.80b}$
Caloric value	$= 580 \text{ calories} \cdot \text{g wet weight}^{-1c}$
<i>Algae</i>	
Wet weight (μg)	$= 10^6 \mu\text{m}^{3d}$
Caloric value	$= 1000 \text{ cal} \cdot \text{g wet weight}^{-1c}$

^aWalz (1979).

^bWalz (1978a).

^cMean of values reported in Stanczykowska and Lawacz (1976), Birger and Maljarewska (1965, cited in Stanczykowska and Lawacz (1976)), and Dorgelo and Smeenk (1988).

^dPeters and Downing (1984).

^eIntermediate between values reported in Peters and Downing (1984) and Cummins and Wuycheck (1971).

a maximum consumption rate over a broader range of temperatures, from 8 to 20°C. I fit a temperature-dependence function from Thornton and Lessem (1978) to the data of Walz (1978a) and Reeders and Bij de Vaate (1990), with optimal consumption from approximately 12 to 20°C (Fig. 2).

For the exponent of the weight-dependence function, I used data from Reeders and Bij de Vaate (1990) on the weight dependence of filtration rate. They estimate b_c as -0.39. This is similar to a mean value of b_c of -0.384 for a large number of marine suspension feeding bivalves and a value of -0.393 for *Mytilus edulis*, both reported in Bayne and Newell (1983).

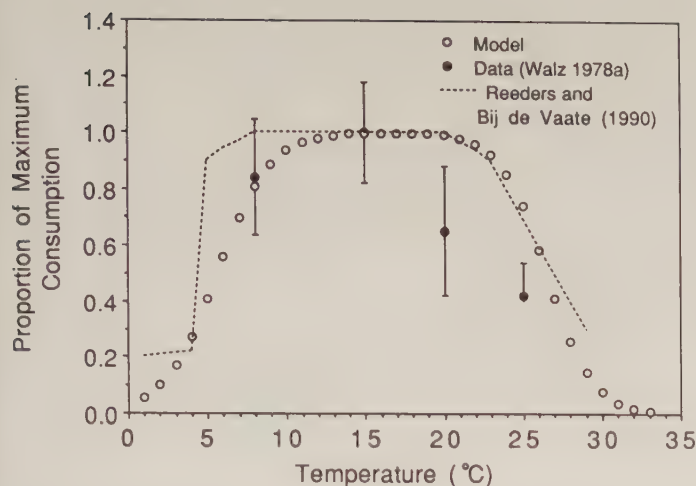


FIG. 2. Consumption, as a proportion of maximum, versus temperature, as reported in Walz (1978a) $\pm$ 95% CI, Reeder and Bij de Vaate (1990), and as modelled. Model points are from the temperature-dependence function described by Thornton and Lessem (1978) with parameters from Table 1.

The intercept for the maximum consumption rate of a 1-g zebra mussel was taken from Walz (1978a) and reflects the average daily feeding bouts of zebra mussels of $16.8 \text{ h} \cdot \text{d}^{-1}$.

The P -value is a multiplier, ranging from 0 to 1, which scales realized consumption as a proportion of the maximum possible consumption. It allows the modelling of growth and consumption under changing conditions of food availability. It essentially describes a linear functional response of an organism to variable food concentrations. Sprung and Rose (1988), Dorgelo and Smeenk (1988), and Walz (1978a) all reported a linear functional response of *Dreissena* to increasing food concentration below the incipient limiting concentration, making the P -value appropriate for modelling realized consumption rates.

Egestion

Egestion is modelled as a function of consumption:

$$(4) \quad F = \alpha_f e^{(\gamma_f P - \text{value})} \cdot C$$

where α_f is the intercept for the proportion of consumption egested versus proportion of maximum consumption realized, γ_f is the coefficient for the dependence of egestion on P -value, and C is consumption in grams per gram per day.

Walz (1978a) reported egestion (true feces) as 76.3% of consumption when *Dreissena* was fed at maximum rates. Walz (1978a) found no relation between assimilation efficiency and the size of the mussel. It is likely, however, that at consumption rates lower than the maximum, the proportion of ingested ration egested is lower. Bayne et al. (1976) summarized work on absorption efficiency in *Mytilus*, which suggests that efficiency is lower at higher ration. In the *Dreissena* model, the proportion of ingested food lost as feces ranges from 31.5% at low ration to 76.3% at maximum ration, spanning a range similar to that of *Mytilus* (Bayne et al. 1976).

Excretion

Excretion is modelled as a constant fraction of assimilated food, independent of size, temperature, and consumption rate. There are no data on excretion rates for *Dreissena*, so I have used those measured for *Mytilus edulis* from Bayne and Newell

(1983) of $0.064 \cdot (C - F)$ where C is consumption and F is egestion in grams per gram per day.

Implementation of the Model

Several data sets are needed to run the model. The first includes the species-specific physiological parameters described above. Then, several data sets describing environmental conditions are needed, including food availability and temperature. Finally, because the currency of the bioenergetics model is calories, the caloric densities of the zebra mussels and food are required. The conversions used for caloric density are listed in Table 2.

Validation of the Model

To validate the bioenergetics model, independent estimates of consumption and growth and the temperature history of the modelled organism must be known (Rice and Cochran 1984). Because daily consumption rates are difficult to obtain, there are few independent measures of growth and consumption against which to test the model.

I have used an alternative approach to estimate consumption rates independently of model assumptions, allowing a test of the model. This approach takes advantage of the well-described functional response of zebra mussels to increasing food concentration (Walz 1978a; Dorgelo and Smeenk 1988; Sprung and Rose 1988). Filtration is initiated at a threshold concentration and is maintained at a constant rate over a wide range of food availability. At some higher, incipient limiting concentration, filtering rate declines. This response of filtering rate to food concentration results in a linear functional response of ingestion up to the limiting concentration, with constant ingestion rates at higher food concentrations. A similar pattern has been reported in *Mytilus edulis* (Foster-Smith 1975). I used this functional response to estimate consumption rates from easily obtained data on phytoplankton abundance.

In his detailed studies of the zebra mussel in Lake Constance, Walz (1978a, 1978d) presented the necessary information for validating the bioenergetics model. He presented information on the functional response of the zebra mussel to increasing food concentration (Walz 1978a) and data on food availability, temperature, and growth of zebra mussels in Lake Constance. In these experiments, Walz (1978d) measured growth of zebra mussels in laboratory chambers provided with water from two depths in the lake, for two different age classes. Walz (1978a) measured the functional response of zebra mussels in terms of particulate carbon and reported an incipient limiting concentration of $2 \text{ mg} \cdot \text{C} \cdot \text{L}^{-1}$. I assumed a linear response through the origin. Thus, at carbon concentration less than $2 \text{ mg} \cdot \text{L}^{-1}$, $P\text{-value} = (C/\text{limiting concentration})$. Above $2 \text{ mg} \cdot \text{L}^{-1}$, consumption is maximal at a P -value of 1. None of the data used to validate the model were used to establish the parameters, so this serves as an independent test of the model.

I compared modelled growth with observed growth of zebra mussels under environmental conditions of both the surface and 60-m depths in Lake Constance. At the surface conditions, I tested the model against data for two year classes of mussels.

Temperature and food availability were read from the graph provided in Walz (1978d). Food availability was averaged over 1-mo intervals and converted to P -values. The temperature on any day was estimated by interpolation from known values. The model was run for 1-mo time intervals corresponding to the periods of constant P -values. The weights of zebra mussels, reported as milligrams carbon dry soft body weight (Walz



FIG. 3. Location map of sites in the Great Lakes for which zebra mussel growth was modelled, and sites of source data for temperature and phytoplankton abundance.

1978d), were converted to wet soft body weight using the conversions in Table 2. For the second year class in Lake Constance, Walz (1978d) measured spawning losses independently of whole-animal weight loss as approximately 5% of dry body weight. Spawning was included in the model as a step function wet weight loss of $0.05 \cdot d^{-1}$, occurring on June 1, with the assumption that the water content of the animal and eggs was the same.

The initial conditions for the model were set to the April 1 data for the young-of-the-year (YOY) cohort and to January 1 data for the previous year's (1+) cohort. This is the only date on which the model was constrained to the observed values; following that date, observed and model predictions were independent.

Application to the Great Lakes

The bioenergetics model can predict the growth of zebra mussels in novel habitats and thus help predict the ultimate range of the zebra mussel in the Great Lakes. I used the model to simulate growth in nearshore areas of Lakes Erie, Michigan, Huron, Ontario, and Superior (Fig. 3). In order to examine how zebra mussel growth would respond to localized conditions in one lake, I modelled growth in two areas of Lake Superior: the oligotrophic northwest shore and the more mesotrophic Duluth/Superior Harbor area.

Using an initial weight of 0.03 g, a weight similar to that of recently settled zebra mussels (Walz 1978d), zebra mussel growth was simulated for the first year of life. Simulations were started in August and run through July, before spawning takes place. Temperature (Bennet 1978; Boyce et al. 1977; Millar 1952; McCormick 1990; Ohio Department of Natural Resources 1961) and phytoplankton biomass data (Munawar and Munawar 1978; Gray 1987; Makarewicz 1987, 1988; McCormick 1990) were taken from the literature for nearshore areas where available. Phytoplankton biomass was converted to a P -value, or feeding rate, using the functional response described in Sprung and Rose (1988) in which zebra mussels fed at maximum rates at phytoplankton concentrations of $1.25 \text{ g} \cdot \text{m}^{-3}$. This func-

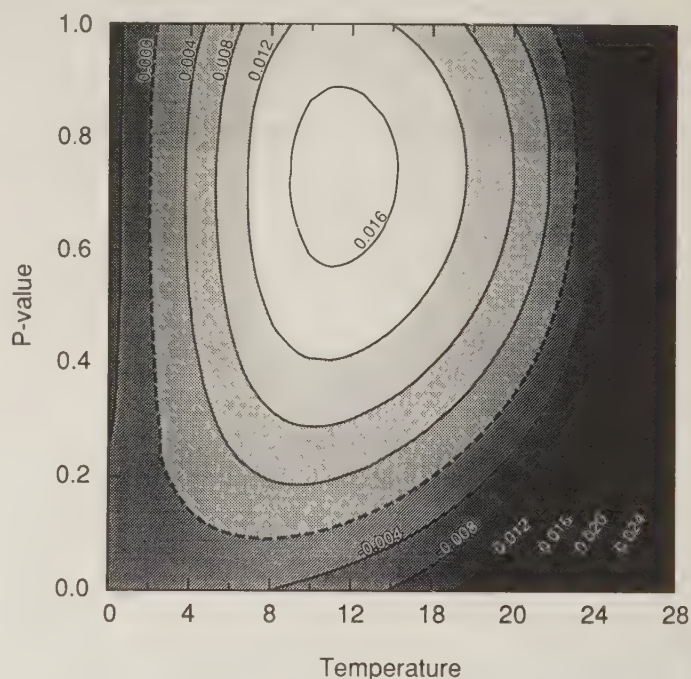


FIG. 4. Isopleths of specific growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) in relation to temperature ($^{\circ}\text{C}$) and P -value for a 0.1-g zebra mussel.

tional response was used rather than that of Walz (1978a) because Great Lakes food availability was measured as phytoplankton biomass rather than particulate carbon.

Results

Below, I first describe the general features of the bioenergetics model, in particular the dependence of growth on temperature and food availability under constant conditions. I then describe the validation of the model, and finally report predicted growth rates of zebra mussels in the Great Lakes.

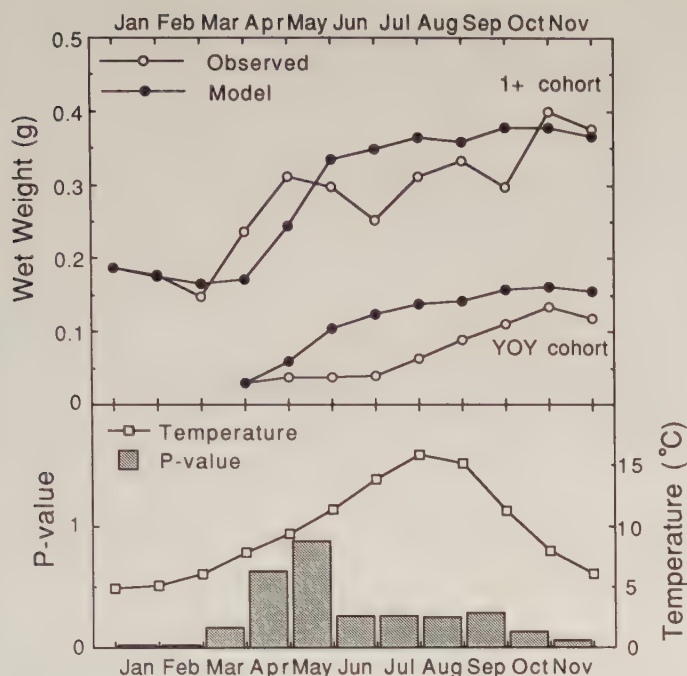


FIG. 5. Environmental conditions and growth of YOY and 1+ cohorts of zebra mussels in surface water from Lake Constance. Temperature and *P*-value and observed weight are calculated from Walz (1978d). The model was constrained to the initial weight on January 1 for the 1+ cohort and April 1 for the YOY zebra mussels. Weight is for soft body only.

Modelled growth of zebra mussels is dependent on temperature and food availability (Fig. 4). Optimal growth occurs at 11°C. For a 0.1-g animal feeding at maximal consumption rates, maintenance rations are not met above 25°C and growth stops. Because assimilation efficiency decreases with increasing ration, growth is optimal at a consumption rate 80% of the maximum. This is a response typical of suspension feeders, whose ability to process food is overwhelmed at high concentrations of suspended material.

Evaluation of the Model

I have compared modelled growth with observed growth of zebra mussels in Lake Constance. At 60 m, conditions over the year are relatively constant, with a temperature of 5.2°C and a food availability corresponding to a *P*-value of 0.0335.

Conditions are more variable for the surface zebra mussels. Temperature ranges from 5 to 16°C and food availability from 0.05 to >2 mg C·L⁻¹. The changing temperature and food conditions are shown in the lower panel of Fig. 5.

The zebra mussel bioenergetics model yields a reasonable fit to observed growth for zebra mussels in Lake Constance. Under the constant conditions at 60 m, zebra mussels were observed to lose weight throughout the year. Figure 6 presents observed and model growth over 1 yr. The initial weight of 0.347 was taken from a regression line plotted by Walz (1978d) through his growth rate data. The model predicts observed weight loss within 6% after 1 yr of growth.

Modelled growth appears to closely follow observed growth under surface conditions as well (Fig. 5). Final weight is modelled to within 32% for YOY zebra mussels and 3% for the 1+ cohort. For the 1+ cohort the model shows a peak in growth during the spring, during high food availability and moderate temperatures. Periods of observed weight gain or loss

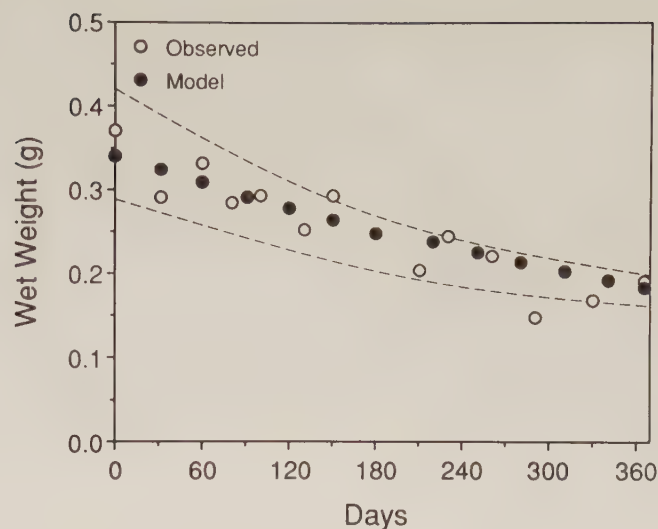


FIG. 6. Zebra mussel growth in water from a depth of 60 m in Lake Constance. Observed values are from Walz (1978d) and are means of 16 zebra mussels. Initial weight for the model run was taken from a regression calculated through the observed points (Walz 1978d), and the model was run at a constant *P*-value of 0.0335 and a temperature of 5.2°C. Weight is for soft body only.

do not always coincide with model predictions, however. To test for consistent bias in the model, I examined how differences in predicted and observed growth over 1-mo intervals were related to temperature, food availability, or season. Residuals were calculated as the predicted weight change in the model minus the observed weight change over 1-mo growth intervals (Fig. 7a). For this analysis, independent runs of the model were performed for each of 11 dates so that errors from one month's simulation would not propagate through the rest of the simulations. An analysis of the residuals of modelled versus observed growth revealed no directional bias in the model in relation to temperature (Fig. 7b) or body size (Fig. 7d). Regression of residuals on temperature and size are insignificant for both year classes (Table 3). To look for nonlinear, seasonal bias, I also performed a second-order polynomial regression of residuals on temperature. These, too, are insignificant for both year classes (Table 3). For the YOY size class, growth tends to be overestimated at high *P*-values and underestimated at low *P*-values. However, this statistical effect is due entirely to growth during May. If the May point is not considered, there is no relation between *P*-value and residual growth ($n = 7$, $df = 6$, $F = 1.639$, $r^2 = 0.247$, $p = 0.257$). As discussed below, May is a period of high food availability but poor food quality (Walz 1978d), so the tendency of the model to overestimate growth is probably a function not of food quantity, but quality, which is not included in the model.

Application to the Great Lakes

Growth

Based on the reported values for phytoplankton availability and water temperatures from a variety of sites, zebra mussel growth is predicted to vary widely in the Great Lakes (Fig. 8). Annual modelled growth is -0.005 g·yr⁻¹ along the northwest shore of Lake Superior but 0.262 g·yr⁻¹ along the north shore of Lake Ontario. These differences in absolute growth primarily reflect the trophic gradient present in the Great Lakes, which spans over an order of magnitude in phytoplankton biomass. Maximum monthly mean phytoplankton biomass is 1.94 g·m⁻³

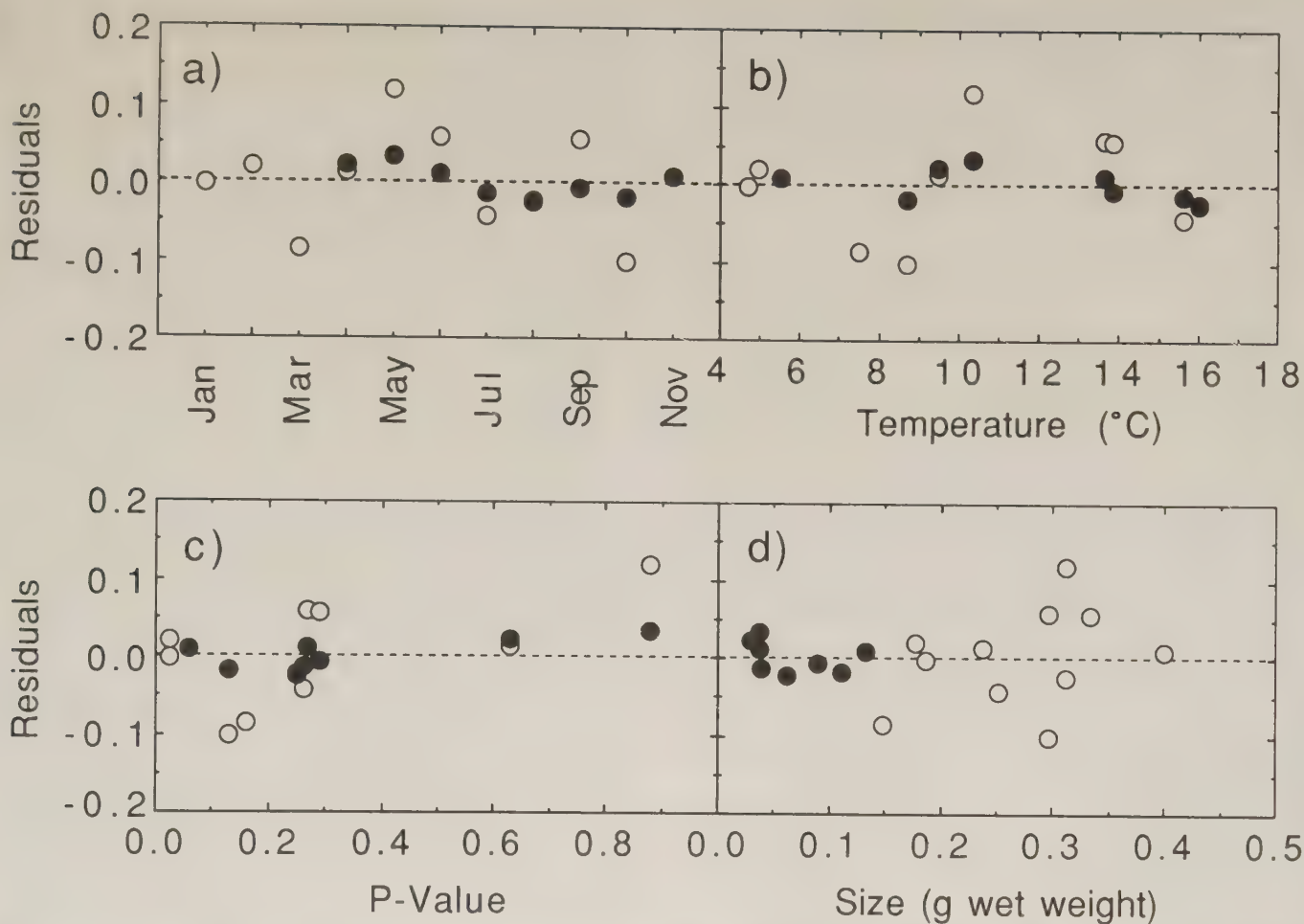


FIG. 7. Modelled growth residuals (monthly weight increment minus observed monthly weight increment, Walz 1978d) for Lake Constance zebra mussels versus (a) month, (b) temperature, (c) *P*-value, and (d) size. Solid circles are YOY and open circles are 1+ zebra mussels.

TABLE 3. Analysis of growth residuals.

Cohort	<i>n</i>	df	Order	Independent variable	<i>F</i>	<i>r</i> ²	<i>p</i>
YOY	8	7	1	Temperature	1.625	0.213	0.249
			2		1.757	0.413	0.264
			1	<i>P</i> -value	7.311	0.549	0.035
			1	Size	0.918	0.133	0.375
1+	11	10	1	Temperature	0.092	0.010	0.769
			2		0.128	0.031	0.881
			1	<i>P</i> -value	4.176	0.317	0.071
			1	Size	1.189	0.117	0.304

in Lake Ontario but only $0.177 \text{ g} \cdot \text{m}^{-3}$ along the northwest shore of Lake Superior. With increasing food availability, annual growth increases from Lake Superior to Lake Erie. Lake Ontario, however, has lower phytoplankton biomass than Lake Erie, yet higher growth rates. This reflects the different temperature regimes in the two lakes. Lake Erie is warmer, and summer temperatures exceed the maximum at which zebra mussel growth can be supported (Fig. 4). Lake Ontario, on the other hand, has maximum temperatures closer to those optimal for growth.

While absolute zebra mussel growth differs among the Great Lakes, the seasonal pattern of growth is fairly consistent and reflects the relation between temperature and growth. In general, zebra mussels experience positive growth in spring and

fall in each of the Great Lakes (Fig. 9). During these periods, high phytoplankton biomass associated with spring and fall turnover coincides with moderate temperatures near the growth optimum. Even under conditions of high food availability, growth rates typically decline from May or June until midsummer and increase again in August and September as temperatures begin to decline. In all of the lakes, zebra mussels lose weight in winter under conditions of low food availability and low consumption rates. This predicted bimodal growth pattern is confirmed by the field studies of Morton (1969) and Walz (1978d).

Consumption

Hamburger et al. (1990) estimated the ingestion rate of *Dreissena polymorpha* in Lake Esrom, a moderately eutrophic lake. They estimated that over a 180-d growth season, an individual mussel ingests 1.12 kcal. I have made a similar estimate for Lake Constance and the Great Lakes (Table 4). In the eutrophic lakes in this group, Lakes Constance, Erie, and Ontario, modelled ingestion is comparable with estimated ingestion in Lake Esrom. In the more meso- and oligotrophic lakes, ingestion rates are lower.

Discussion

The zebra mussel bioenergetics model yields a reasonably good estimate of observed growth for zebra mussels in Lake Constance. This correspondence suggests that the functional

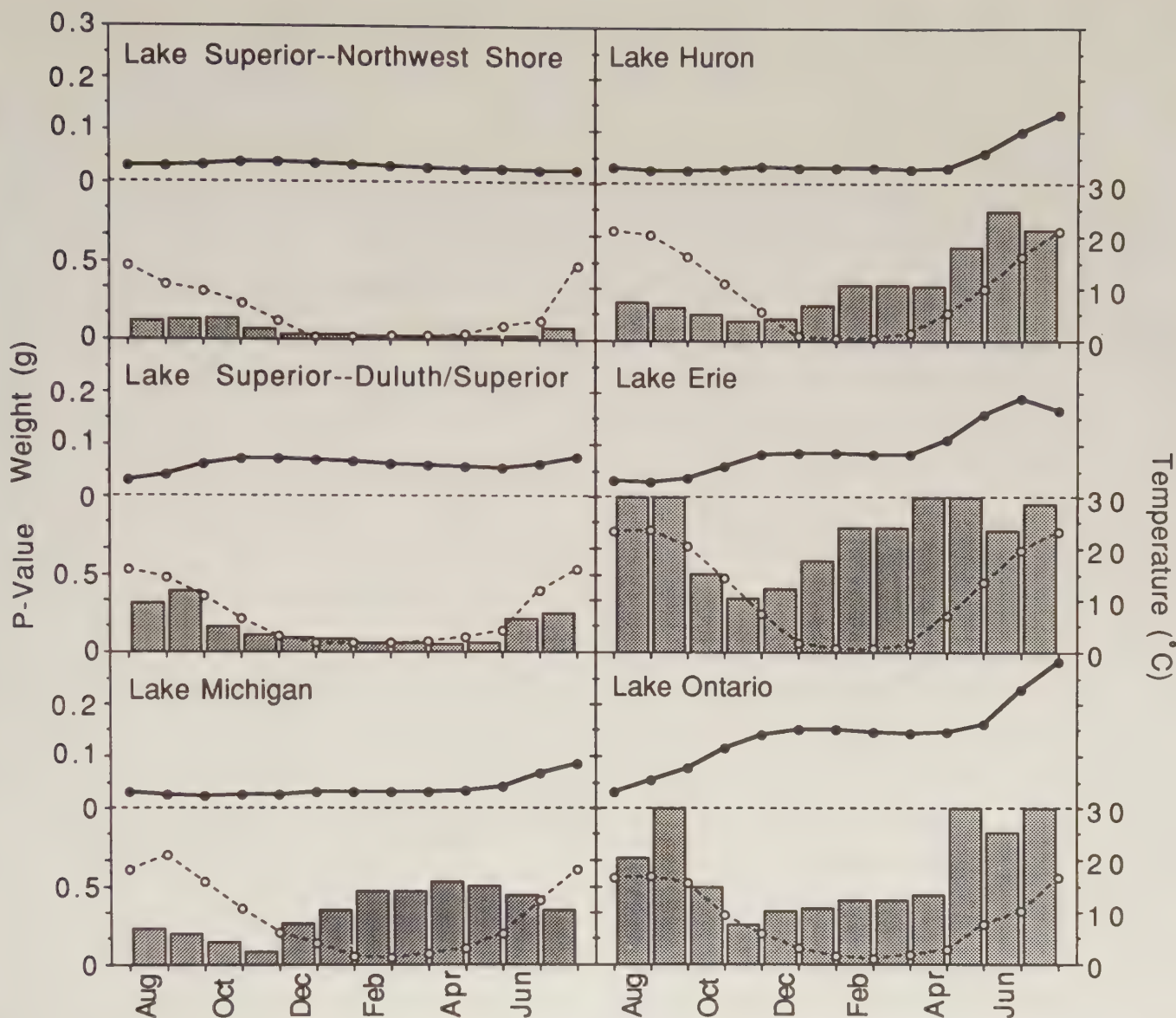


FIG. 8. Temperature (open circles), P-value (bars), and modelled growth (solid circles) of zebra mussels in the Great Lakes. All zebra mussels were started with an initial weight of 0.03 g on August 1.

response of consumption to food availability provides a powerful tool for predicting zebra mussel consumption rates and growth. Most previous uses of these bioenergetic models in studies of fishes have been constrained by information on field consumption rates (Rice and Cochran 1984). Post (1990) made an initial step in demonstrating that the proportion of maximum consumption (P -value) can be modelled as a functional response. He showed that P -values fit to known growth end points of YOY yellow perch (*Perca flavescens*) are highly correlated with zooplankton abundance, demonstrating that functional responses can be calculated post facto from model simulations. I have developed a functional response from independently derived data and applied it a priori to model growth. This approach allows the estimation of growth and consumption of zebra mussels in novel environments, or where growth rate is difficult to measure. This approach may be generally useful for predicting the ecosystem effects of exotic organisms.

The way in which the model was tested, constraining the model to an initial observation, has great potential for the propagation of model error (Bartell et al. 1986). That the fit was

reasonably close throughout the year suggests that there are no systematic errors in the model.

Over the course of the year, however, there are large differences between predicted and observed growth (Fig. 7a), although there appears to be no systematic bias toward over- or underestimation of true growth in relation to temperature (Fig. 7b), size (Fig. 7d), or food availability (Fig. 7c).

The differences between the model and the observed data may also be explained by several factors which are not taken into account in this model. The first is food quality. The model considers all diet items to be identical, both in caloric value and digestibility. It is known, however, that zebra mussels are selective feeders and reject many particles in pseudofeces (Ten Winkel and Davids 1982). The period of greatest model overestimation of growth in Lake Constance is during May (Fig. 6). Particulate carbon reaches high values during this period (Fig. 6), and zebra mussels are consequently feeding near their maximum rates in the model. This peak in carbon is caused primarily by a bloom of *Stephanodiscus hantzschii*, which replaces *Rhodomonas* spp. in an earlier bloom (Walz 1978d).

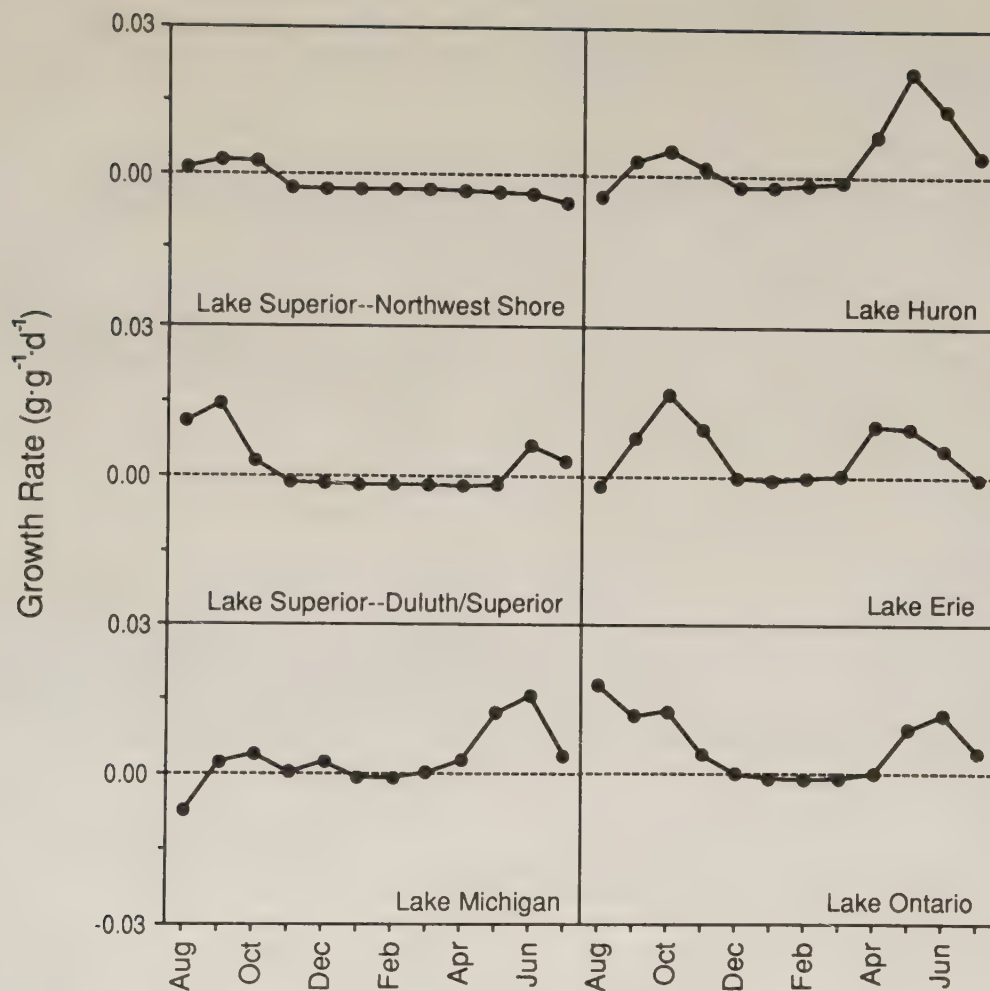


FIG. 9. Specific growth rates of zebra mussels modelled over monthly growth increments for the Great Lakes.

TABLE 4. Estimated ingestion rates for zebra mussels over the growth season compared with modelled lakes.

Lake	Ingestion (kcal·ind ⁻¹ ·180 d ⁻¹)
Lakes from Hamburger et al. (1990)	
Esrom	1.12
Mikolajskie ^a	1.82
Modelled lakes (this study)	
Constance	1.08
Ontario	1.58
Erie	1.52
Huron	0.54
Michigan	0.24
Superior (Duluth)	0.26

^aCalculated by Hamburger et al. (1990) from data in Stanczykowska et al. (1975).

Walz (1978d) suggested that *Stephanodiscus* may have lower nutritional value for *Dreissena*. This may account for some of the model overestimation of growth.

Differences between modelled and observed growth may also contain information on the apportionment of resources by zebra mussels to body or shell growth. The allometry of feeding and respiration in molluscs is based on the relations among surface, volume, and mass of the soft body (Bayne and Newell 1983), and parameters in this model are all based on soft body weight.

However, mussels apportion large, but poorly known, amounts of energy to shell growth (Wilbur and Saleuddin 1983). If the model is sufficiently well characterized, the energy of shell deposition can be estimated by the difference between modelled and observed growth.

The overall poorer fit for the YOY cohort may result from interactions among the above factors. Seasonal mean phytoplankton biomass may be a poorer estimate of food availability for the smaller zebra mussels. If smaller zebra mussels can use a smaller fraction of the total food than larger zebra mussels, growth would be overestimated. Alternatively, small zebra mussels may be apportioning a greater proportion of their energy into shell growth than large zebra mussels.

Consumption can be estimated by fitting a *P*-value to a known growth increment. In this model, it can also be estimated from the food availability and the functional response curve. Error analysis of similar bioenergetic models (Bartell et al. 1986) suggests that uncertainty in the estimation of model parameters leads to greater error in the estimation of growth from initial conditions than in the estimation of consumption between two known growth points. This suggests that estimates of consumption should differ greatly in each of these two ways of implementing the model. In the zebra mussel model, however, there is little difference between estimates of consumption under these two modelling scenarios. Cumulative annual consumption predicted for the 1+ cohort of zebra mussels in Lake

Constance, based on fitting consumption to known growth, is $1.24 \text{ g} \cdot \text{ind}^{-1} \cdot \text{yr}^{-1}$ versus $1.19 \text{ g} \cdot \text{ind}^{-1} \cdot \text{yr}^{-1}$ when based on the functional response and food availability.

Simulated consumption rates based on the functional response and allometry of the zebra mussels agree well with consumption rates arrived at in two other studies using different methods (Table 4). Stanczykowska et al. (1975) estimated consumption rates in the field as the difference between particle removal and feces and pseudofeces production in experimental chambers. Hamburger et al. (1990) used a bioenergetic estimate of respiration and conversion factors for *P/B* ratios and assimilation efficiency. Given the unknown importance of zebra mussel impacts on phytoplankton resources and Great Lakes food webs, this model result offers a potentially valuable forecasting tool. Given the size structure of the zebra mussel population and its abundance, the model can estimate total herbivory at the site or whole-lake scale. Filtration rates extrapolated from food abundance and modelled estimates of ingestion are within the range of those observed for *Mytilus* but at the higher end of those observed for zebra mussels by other workers (Bayne and Newell 1983; Kryger and Riisgård 1988). A more appropriate estimate of filtration rates requires consideration of local depletion effects, food quality, and selective feeding and calls for careful experimentation and extension to modelling applications.

Model predictions of growth will depend on the particular functional response used to estimate consumption rates from food availability. For the Great Lakes, I have used a functional response based on feeding rates on a unialgal suspension of *Chlamydomonas reinhardtii* (Sprung and Rose 1988). Because zebra mussels are selective feeders, the functional response will depend on the particular assemblage of algae the zebra mussel is exposed to. Experiments describing the functional response of zebra mussels to a more realistic assemblage of algae and organic particulate matter would increase the accuracy of growth estimates.

Because pseudofeces are not included in the current model, consumption rates underestimate the effect of zebra mussels on the phytoplankton. Consumption rates are based solely on ingestion rate, rather than filtration rate. Depending on the food particles and their concentration, zebra mussels can filter twice as much material as they actually ingest (Walz 1978a), the remainder being ejected as pseudofeces. Nevertheless, much of the phytoplankton in pseudofeces is effectively removed from the water column. For the model to accurately reflect the impact of zebra mussels on phytoplankton dynamics and sedimentation rates, pseudofeces must eventually be included.

While a number of factors will determine whether zebra mussels reach high densities in any particular area of the Great Lakes, temperature, food availability, and substrate availability are probably the most important. The bioenergetics model, by integrating temperature and food availability into estimates of potential growth rates, can predict in which lakes zebra mussels may reach high densities, given suitable substrate.

The population growth rate of zebra mussels will depend, to a great extent, on the growth rate of the individual animals. Female reproductive rate is dependent on the size of the mussel (Walz 1978b). Using the regression for female reproductive rate from Walz (1978b), the expected reproductive rate of zebra mussels in the Great Lakes ranges from 0 along the northwest shore of Lake Superior to $20\,000 \text{ eggs} \cdot \text{ind}^{-1} \cdot \text{yr}^{-1}$ in the Duluth/Superior region to $90\,000 \text{ eggs} \cdot \text{ind}^{-1} \cdot \text{yr}^{-1}$ in Lake Ontario. These estimates of egg and veliger production based on growth can be coupled to spatial models of zebra mussel

distribution to examine the effects of zebra mussels on phytoplankton biomass or contaminant cycling at local, regional, or lakewide scales.

While growth rates are predicted to be low in oligotrophic lakes like Lake Superior, localized regions of higher productivity may well support zebra mussels. For instance, annual growth in the Superior/Duluth region of Lake Superior was predicted to be comparable with growth in Lake Michigan. Similarly, growth rates in areas such as Green Bay in Lake Michigan and Saginaw Bay in Lake Huron may well be much higher than that predicted for the main lake.

This model can also be used to help site the location of water intake pipes to reduce the probability of fouling with zebra mussels. Optimal sites would be in regions with low temperature and food, where zebra mussel growth is slow. Thus, this model can help predict the proper location for intake pipe placement, minimizing zebra mussel growth rates, and reducing the cost and side effects of chemical treatment for zebra mussel removal.

For this model to be locally applicable, the local onshore-offshore productivity gradients, the effects of point sources of nutrients, and the water circulation patterns surrounding zebra mussel beds must be known. However, the general functional response of zebra mussels and the encouraging first results of independent tests of the model lend strong support to this approach for predicting the growth, spread, and food web effects of zebra mussels and other invaders in the Great Lakes.

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Application of Diel Feeding Chronology to Habitat Suitability Analysis of Warmwater Stream Fishes

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Diel feeding chronology and daily ration were determined from stomach or foregut contents of common carp (*Cyprinus carpio*), golden redhorse (*Moxostoma erythrurum*), channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), and longear sunfish (*Lepomis megalotis*) in the Vermilion River, Illinois. Feeding was highly variable among individuals, hours, and months for each species. Discontinuous feeding was detected in common carp, golden redhorse, and channel catfish. Common carp and the two centrarchid species fed with greatest intensity near sunrise and sunset; golden redhorse and channel catfish feeding was highest at night. Daily ration estimates were higher for fishes with stomachs than those for stomachless species. Microhabitats occupied by fish over the diel period were identified using nondisruptive techniques: direct observation, prepositioned electrofishing, and radiotelemetry. Microhabitat use during high-feeding periods was significantly different ($P \leq 0.10$) than that during low feeding for at least one habitat variable in each species examined. Association with cover also varied between feeding regimes. Our findings suggest that realism of instream flow assessments may be improved if habitat suitability criteria are stratified by feeding regime.

Nous avons déterminé, à partir du contenu des estomacs et de la partie antérieure du tube digestif, la chronologie nyctémérale de l'alimentation et la ration quotidienne de carpes (*Cyprinus carpio*), de suceurs dorés (*Moxostoma erythrurum*), de barbus de rivière (*Ictalurus punctatus*), d'achigans à petite bouche (*Micropterus dolomieu*) et de crapets à longues oreilles (*Lepomis megalotis*) de la rivière Vermilion, en Illinois. L'alimentation de chaque espèce présentait une grande variabilité en fonction des individus, de l'heure et du mois. Une alimentation discontinue a été notée chez les carpes, les suceurs dorés et les barbus de rivière. Les carpes et les deux espèces de centrarchidés s'alimentaient avec le plus d'intensité aux environs du lever et du coucher du soleil tandis que les suceurs dorés et les barbottes de rivière s'alimentaient surtout la nuit. Les rations quotidiennes estimées étaient plus élevées chez les poissons possédant un estomac proprement dit. Les microhabitats occupés par les poissons au cours d'une période nyctémérale ont été déterminés par techniques non perturbatrices: observation directe, pêche électrique à équipement déjà en place et radiotélémétrie. Pour chaque espèce et au moins une variable liée à l'habitat, les microhabitats utilisés pendant les périodes d'alimentation intensive différaient de façon significative ($P \leq 0,10$) de ceux des périodes de faible alimentation. Le facteur d'association avec le couvert variait aussi en fonction des régimes d'alimentation. Nos résultats portent à croire que la stratification par régimes d'alimentation des critères de pertinence de l'habitat pourrait permettre d'accroître l'exactitude de l'évaluation des apports au cours d'eau.

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Little is known of the feeding biology of many warmwater stream fishes, particularly those species of little sport or commercial value. While distinct foraging and resting habitats have been identified for stream salmonids (Gosse and Helm 1982; Fausch 1984), a similar finding has not been well documented in warmwater streams. Nonetheless, predator-prey relationships certainly influence habitat use by warmwater stream fishes (Power and Matthews 1983; Gilliam and Fraser 1987; Gorman 1987; Schlosser 1987). Diel and seasonal changes in habitat use by some species may be attributed to a predator avoidance response, a response to differences in prey availability, or most likely, a complex interaction of both factors (Cerri 1983; Cerri and Fraser 1983). Such variability in activity

and habitat use is common in stream fishes and is likely related to predator-prey interactions.

Efforts to determine the effects of flow modifications on stream habitat and biota have yielded a variety of models and techniques (Morhardt 1986), none of which incorporates the feeding dynamics of fishes. Orth (1987) recognized the Instream Flow Incremental Methodology (IFIM), described by Bovee (1982), as state of the art. Although widely used in stream habitat assessment (Reiser et al. 1989), a growing body of evidence indicates the existing habitat assessment techniques, including the IFIM, are problematic when applied to warmwater streams (Gore and Nestler 1988; Osborne et al. 1988; Bain and Boltz 1989). Furthermore, limited predictive abilities

of the IFIM, due mainly to a lack of correlation between estimated available habitat and fish biomass, have led to disagreement on its correct application (Mathur et al. 1985; Orth 1987; Gore and Nestler 1988).

The IFIM incorporates species biology into hydraulic models using univariate functions referred to as probability-of-use, utilization, suitability, or preference curves (Bovee and Cochnauer 1977; Bovee 1986). Orth (1987) offered ecological considerations including energetics, food limitation, and predation risk that may improve biological realism in the development and application of instream flow and habitat models. He noted that the unique features of foraging and resting sites are not adequately described by present habitat suitability functions which do not distinguish between seasons or activities such as feeding. Orth (1987) recommended that habitat variables that describe food availability must be sought and that instream flow assessments include site-specific habitat criteria that reflect the local adaptations of fishes to predators.

In this paper we examine the diel feeding and habitat use for five fish species of a prairie stream and develop a procedure for incorporating feeding dynamics into the development of habitat suitability criteria. As part of this study we (1) determine feeding chronology and daily ration of fishes in the field and distinguish high-feeding and low-feeding intervals of the diel cycle, (2) develop on-site habitat suitability criteria for the same species, and (3) develop distinct habitat suitability criteria by temporally stratifying feeding regime (high or low). Finally, we compare these suitability functions to determine if microhabitat use differs between high- and low-feeding periods and discuss the implications of our findings with regard to habitat suitability analysis.

Study Area

The study was conducted in two adjacent branches of the Vermilion River (Wabash drainage) in east-central Illinois. The Salt Fork and Middle Fork of the Vermilion drainage are fifth- and sixth-order streams (sensu Horton (1945) and Strahler (1957)) and drain approximately 1204 and 1109 km², respectively. The watersheds of both streams are primarily agricultural and much of their upper reaches has been channelized to facilitate drainage. The streams drain relatively impermeable soils and receive most of their water from surface and shallow subsurface (field tile) runoff. Detailed descriptions of riparian structure and land use, water quality and temperature, and ecosystem metabolism of the Vermilion drainage basin may be found in Wiley et al. (1990).

Fishes were collected for feeding studies from a 2-km reach of the Salt Fork, located 16 km upstream of its confluence with the Middle Fork. The study reach had a drainage area of 995 km² and a mean slope of 0.76 m·km⁻¹. Microhabitat use data were collected from fishes found throughout the Salt Fork and Middle Fork drainages, but primarily from locations in the lower reaches of each stream. These areas conformed to a typical sequence of shallow riffles, runs, and deep pools (up to 3 m during base flow). Substrates were predominantly coarse gravel, cobble, and boulders in riffles, coarse sand and fine gravel in runs, and silt-sand mixtures in pools.

Methods

Feeding Chronology

Individuals of five fish species, common carp (*Cyprinus carpio*), golden redhorse (*Moxostoma erythrurum*), channel

catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), and longear sunfish (*Lepomis megalotis*), were collected for feeding studies over 24-h periods on 8–10 May, 23–24 July, and 22–23 October 1984. Fish were sampled over two 12-h periods during May and over a single 24-h period in July and October. Mean water temperature (and range) during each 24-h experiment was 14.0°C (12.1–15.0) in May, 26.0°C (24.5–28.0) in July, and 11.3°C (10.2–12.5) in October.

Fish were collected with a boat-mounted, boom-type electrofisher, powered by either a 230-V 3000-W, three-phase alternating current (AC) generator or a 240-V direct current (DC) power source (60 pulses·s⁻¹). Each 24-h experiment consisted of eight 3-h intervals which included a 2-h collection period followed by 1 h of no collecting to assure an adequate time separation between samples. Subsequent collections were made in an undisturbed stream reach upstream of the previously sampled area.

All fish were measured for total length (± 1 mm TL) and weighed (± 1 g), and all species except smallmouth bass were killed and iced. The entire alimentary canal was removed and fixed in a 10% formalin solution and later preserved in 70% ethanol. Stomach contents of smallmouth bass were removed from live fish in the field using Plexiglas tubes (Van Den Avyle and Roussel 1980) and preserved. The fish were then fin-clipped to avoid resampling and released.

Fish numbers and sizes varied among species, experiments, and sampling intervals (Table 1). All fish included in this study were age 1 or older, based on frequency distributions, limited age determination by scale analysis, and size-age relationships found in the literature (Carlander 1969; Pflieger 1975; Carlander 1977; Smith 1979). In the laboratory, preserved contents were removed from the stomachs of channel catfish and longear sunfish and from the foreguts (anterior one third of the alimentary canal) of common carp and golden redhorse. Contents were drained, blotted, and weighed (± 0.1 mg) on a tared analytical balance. A relative content wet weight (RWW) for each fish was calculated as the stomach or foregut content weight divided by the fish body weight and multiplied by 100.

When the RWW for all species and dates was plotted against fish weight, the maximum RWW values at a given size (weight) displayed an inverse relationship with fish weight (Fig. 1a). Individual species plots for common carp, channel catfish, and smallmouth bass also showed a similar inverse relationship between maximum size-specific RWW values and fish weight (e.g. Fig. 1b). No such negative relationship was detected in golden redhorse or longear sunfish data, which may be a function of the more restricted size range of individuals sampled compared with the other taxa examined (Table 1).

To adjust for bias in RWW associated with size of common carp, channel catfish, and smallmouth bass, we regressed the size-specific maximum RWW for each species against the corresponding fish weight using simple linear regression (e.g. Fig. 1b). A RWW adjusted for fish weight (RWW') was calculated for each individual fish by incorporating the linear model into the equation

$$(1) \text{ RWW}' = \text{RWW} \cdot \frac{a + b(W_{50})}{a + b(W_i)}$$

where a is the Y intercept and b is the slope of the linear regression of fish weight on maximum RWW, W_{50} is the median fish weight for the species, and W_i is the weight of the individual fish. RWW' was substituted for RWW in all calculations and plots for common carp, channel catfish, and smallmouth bass. This procedure had a similar effect as analogous methods of

TABLE 1. Summary of results from three diel feeding studies of five fish species in 1984 from the Salt Fork of the Vermilion River, Illinois. Data are sample sizes ($\pm$ SD), total length (TL) ($\pm$ SD) and weight ($\pm$ SD), relative content wet weight (RWW) ($\pm$ SD), percentage of empty stomachs or foreguts, P -value of F -test in one-way ANOVA to test the effect of time on RWW (temporal continuity of feeding), gastric evacuation rate (R), and daily ration (C_{24}) ($\pm$ 95% confidence limits) expressed as RWW. Mean water temperature (and range) during each 24-h experiment was 14.0°C (12.1–15.0) in May, 26.0°C (24.5–28.0) in July, and 11.3°C (10.2–12.5) in October.

Species and month	Total N	Mean interval N	Mean TL (mm)	Mean weight (g)	Mean RWW (g·100 g ⁻¹)	% empty	F -test P	R (h ⁻¹)	C_{24} (%)
Common carp									
May	43	5 (± 4)	464 (± 101)	1567 (± 999)	0.10 (± 0.13)	25.6	0.0774	0.10	0.23 (± 0.10)
July	41	5 (± 3)	469 (± 90)	1337 (± 670)	0.05 (± 0.10)	43.9	0.0099	0.25	0.45 (± 0.25)
October	32	4 (± 3)	506 (± 109)	1950 (± 1161)	0.34 (± 0.25)	6.2	0.0059	0.09	0.74 (± 0.18)
Combined	116	14 (± 6)	478 (± 100)	1592 (± 971)	0.15 (± 0.20)	26.7	0.2118		
Golden redhorse									
May	74	9 (± 1)	320 (± 43)	367 (± 152)	0.10 (± 0.08)	13.5	0.0694	0.15	0.38 (± 0.06)
July	66	8 (± 2)	316 (± 48)	314 (± 89)	0.10 (± 0.10)	33.3	0.0051	0.13	0.31 (± 0.07)
October	78	10 (± 1)	332 (± 35)	391 (± 125)	0.25 (± 0.15)	5.1	0.0006	0.20	1.22 (± 0.14)
Combined	218	27 (± 3)	323 (± 42)	360 (± 129)	0.16 (± 0.14)	16.5	0.0313		
Channel catfish									
May	32	4 (± 3)	359 (± 81)	460 (± 315)	0.34 (± 0.47)	18.8	0.0209	0.27	2.53 (± 1.31)
July	40	5 (± 4)	329 (± 66)	325 (± 207)	1.04 (± 1.47)	17.5	0.2045	0.29	7.73 (± 2.70)
October	22	3 (± 1)	329 (± 93)	351 (± 248)	0.39 (± 0.32)	9.1	0.9468	0.13	1.23 (± 0.58)
Combined	94	12 (± 6)	339 (± 78)	377 (± 262)	0.65 (± 1.06)	16.0	0.0095		
Smallmouth bass									
May	10	1 (± 1)	236 (± 42)	181 (± 102)	0.62 (± 0.72)	0	0.6206	0.32	5.70 (± 4.56)
July	22	3 (± 1)	257 (± 91)	266 (± 246)	0.82 (± 1.09)	0	0.3548	0.32	6.05 (± 2.56)
October	44	6 (± 3)	220 (± 62)	171 (± 208)	0.63 (± 1.00)	20.5	0.9125	0.20	3.17 (± 1.74)
Combined	76	10 (± 3)	232 (± 71)	199 (± 211)	0.68 (± 0.99)	11.8	0.8020		
Longear sunfish									
May	68	8 (± 2)	128 (± 18)	53 (± 23)	0.72 (± 0.98)	8.8	0.8551	0.23	3.81 (± 1.34)
July	65	8 (± 3)	130 (± 20)	54 (± 22)	0.66 (± 0.97)	13.8	0.1372	0.18	2.93 (± 1.14)
October	35	4 (± 3)	126 (± 18)	50 (± 31)	0.49 (± 0.77)	31.4	0.7546	0.22	2.00 (± 1.02)
Combined	168	21 (± 3)	128 (± 19)	53 (± 24)	0.65 (± 0.94)	15.5	0.9366		

adjustment for size proposed by other investigators (Knight and Margraf 1982; Herbold 1986). Differences between RWW and RWW' in our study, however, were minimal due to the relatively restricted size ranges of fish (e.g. Fig. 1b and 1c).

Mean daily rations (C_{24}) were calculated for each species and date using the method of Elliot and Persson (1978):

$$(2) \quad C_{24} = \sum_{i=1}^m \frac{(S_{(i+1)} - S_i e^{-RT}) RT}{1 - e^{-RT}}$$

where S_i and $S_{(i+1)}$ are the mean RWW of a fish group at the time of successive sampling intervals i and $i+1$, respectively, R is the gastric evacuation rate for the species on that date, T is the time interval between successive samples ($T = 3$ h), and m is the number of sampling intervals in the 24-h experiment ($m = 8$).

R was estimated as the slope of the relationship between digestion rate (r) and mean RWW (S_i) of a fish group (Boisclair and Leggett 1985). Because digestion rate is a positive linear

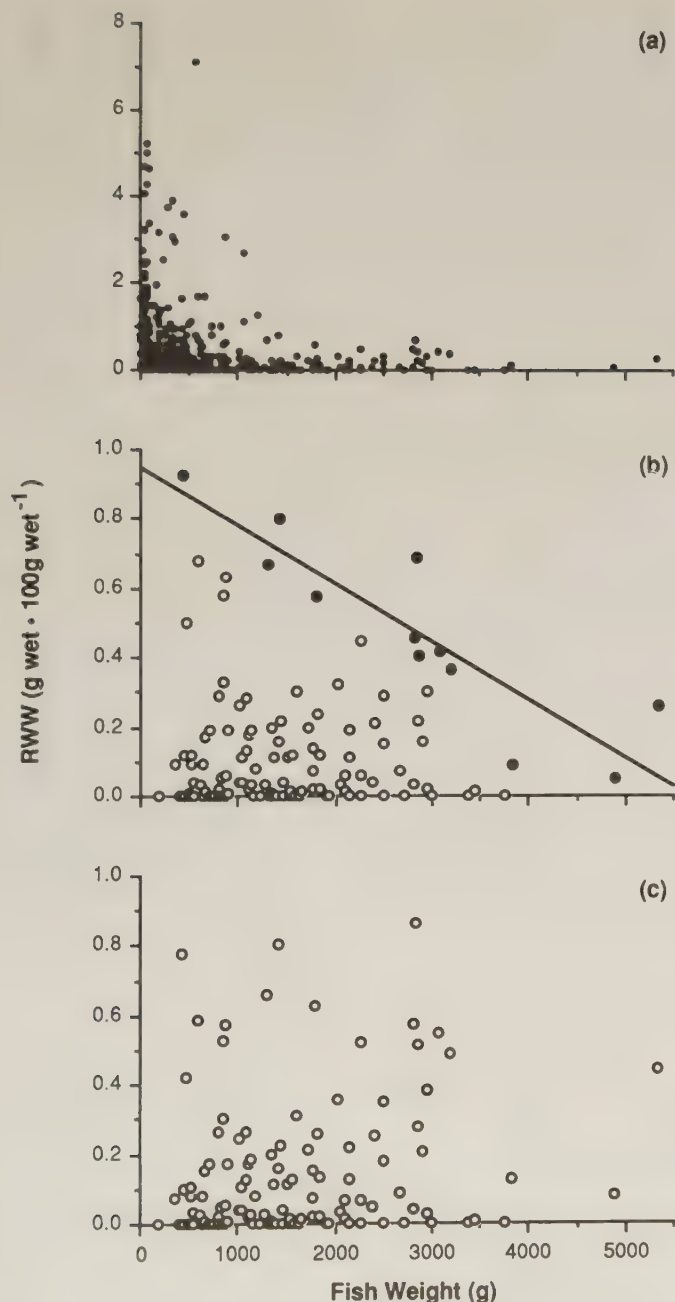


FIG. 1. Plots of relative content wet weight (RWW) versus fish body weight for fishes collected in the Salt Fork of the Vermilion River, Illinois, during three 24-h experiments in 1984. (a) All species plot showing inverse relationship of maximum RWW and fish weight; (b) common carp unadjusted for size showing similar trend; RWW maxima used to derive linear model for adjustment procedure are represented by solid circles; (c) common carp with RWW adjusted for size.

function of fullness that passes through the origin (Elliot 1972), a single observation of that relationship allows the calculation of R . To estimate digestion rate from the decline in stomach or foregut contents, a time of day must be selected during which fish are assumed not to feed. This assumption is best approximated during an interval immediately following a peak in RWW. Thus, species-specific digestion rate r was estimated for each 24-h experiment as

$$(3) \quad r = \frac{S_{(i+1)} - S_{imax}}{T}$$

where S_{imax} is the mean RWW in the interval i of peak mean

RWW over the diel period, $S_{(i+1)}$ is the mean RWW from the subsequent sampling interval, and T is the time interval between successive samples ($T = 3$ h). R was then estimated as digestion rate (r) as a proportion of the peak mean RWW (S_{imax}):

$$(4) \quad R = \frac{r}{S_{imax}}$$

The reliability of this method to estimate R was verified by Boisclair and Leggett (1985) for yellow perch (*Perca flavescens*); they found no significant differences between results of this method and field-derived estimates of R by sequentially sacrificing fish.

Confidence limits were calculated for daily ration estimates using a proportional error estimate in a fashion similar to Post (1990). A mean time-weighted RWW was calculated for each diel experiment and species, and an estimate of its standard error (s) was calculated as

$$(5) \quad s = \left[\frac{1}{m^2} \left(\sum_{i=1}^m \frac{s_i^2}{n_i} \right) \right]^{0.5}$$

where s_i^2 is the variance of the RWW of fish in interval i , n_i is the number of fish sampled in that interval, and m is the number of intervals ($m = 8$). A proportional error was then calculated by dividing s by the mean time-weighted RWW. The 95% confidence limits are the daily ration estimate $\pm$ the product of the daily ration, the proportional error, and the t -score ($\alpha = 0.05$).

To describe a general feeding chronology for each species, a plot of RWW over time was constructed which incorporated combined data from the three 24-h experiments (Fig. 2). One-way analysis of variance (ANOVA) was used to test temporal feeding continuity as determined by changes in RWW of stomachs or foregut contents over time. Differences among sampling interval means were determined using the Tukey (HSD) multiple comparison test (Zar 1984).

Microhabitat Use

Microhabitats used by stream fishes were identified throughout the diel period and periodically throughout all seasons during 1984–85. Approximately one half of the microhabitat data for channel catfish and smallmouth bass (50 and 55%, respectively) were collected during 1980–81. One-way ANOVA revealed no significant differences ($P > 0.05$) between microhabitat use during 1980–81 and 1984–85 for any habitat variable for these species, which justified including the data from earlier years. Fish were located using a combination of three techniques: direct observation, prepositioned electrofishing, and radiotelemetry (Table 2). These techniques were employed because they locate an undisturbed fish during all hours of the day and in a variety of water conditions. Detailed descriptions and evaluations of these techniques can be found in Larimore and Garrels (1985).

Visual observation of fish from the stream bank was enhanced using polarized glasses or binoculars in daylight and a portable light source (Coleman model 220 lantern with reflector) at night. Observations were usually followed by capturing the fish using a Smith-Root type VII DC backpack electrofisher to confirm species identification and to measure the fish.

Electrodes, constructed of two 3-m strands of 12-gauge, solid-core copper wire, were wired to a two-conductor electrical cable and prepositioned in discrete uniform habitats at least 24 h before sampling. The electrodes were positioned nearly

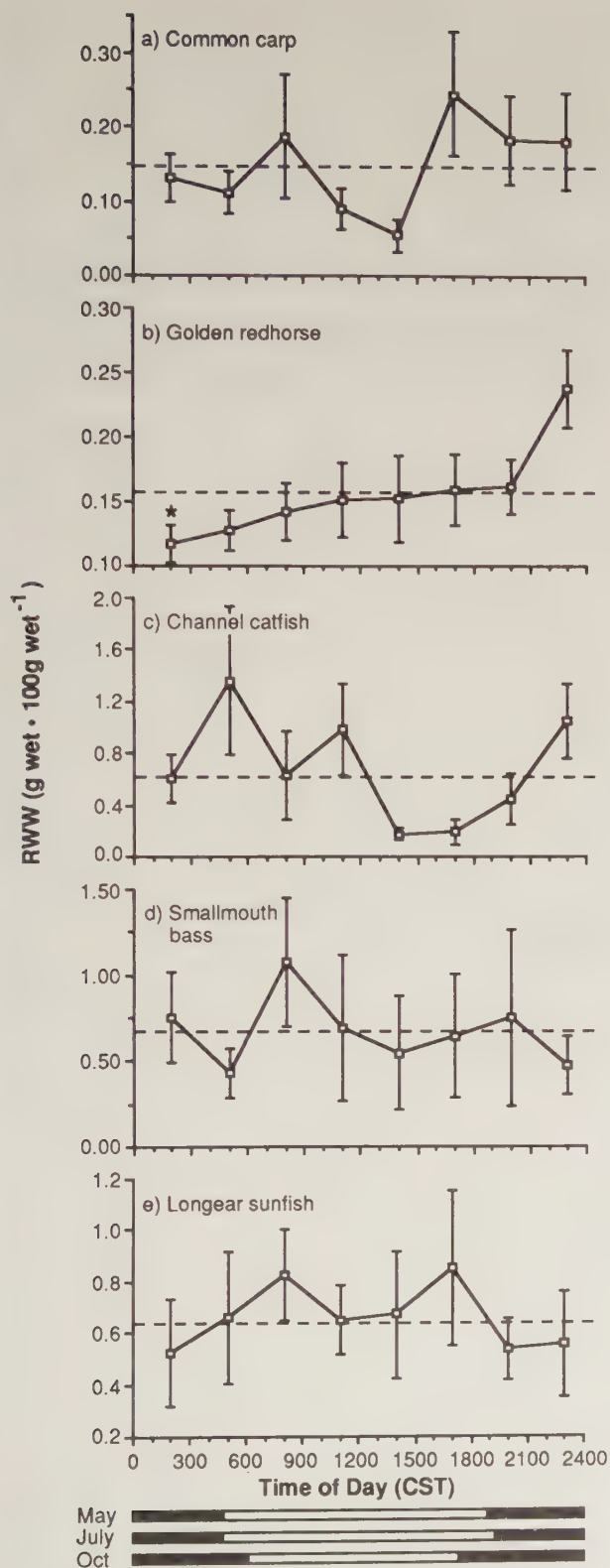


FIG. 2. Diel feeding chronologies of five fishes of the Salt Fork of the Vermilion River, Illinois, as determined from changes in relative content wet weight (mean RWW $\pm$ 1 SE) over time. Plots include the combined results from three 24-h experiments conducted in May, July, and October 1984. Asterisk denotes significantly different mean (Tukey HSD, $P < 0.01$) from that of the previous sampling interval. Horizontal broken lines indicate the unweighted (by interval or month) mean RWW for each species. Open and solid portions of bars represent light and dark hours, respectively, during each 24-h experiment. Sample sizes for each experiment are given in Table 1.

parallel to the direction of flow approximately 0.5 m apart, suspended by wooden stakes, and connected by an extension cord to an AC generator (115-V, 1500-W) located at least 20 m from the stream. In sampling, electrodes were activated, stunned fish collected, and physical habitat characteristics within the electric field were quantified (see below). A 24-h recolonization period was allowed before the electrodes were reactivated.

Radiotelemetry involved the use of internal and external radio transmitters. Small, 50-MHz radio transmitters were attached to fish anesthetized with tricaine (MS-222). Transmitters displaced a volume of 10–12 cm³. Most transmitters were surgically implanted into the body cavities of fish, although some externally attached transmitters were also used. The external transmitter was fixed to a hard plastic saddle roughly molded to fit over the dorsum of a fish. The saddle was adjusted in the field to the individual size and form of a fish. The saddle-mounted transmitter was attached with surgical thread through the dorsum, posterior to the dorsal fin or in a space at the interface of the spinous and soft dorsal fins, where a small portion of fin was clipped. Styrofoam shavings were affixed to approximately adjust the external transmitters to neutral buoyancy. To minimize disorientation and stress, marked fish (numbered Floy anchor tag) were held only until they had recovered from the anesthetic, then released, and subsequently located over a period of several months.

Depth, velocity, substrate, and associated cover were measured after the exact location of a fish was determined by one of the above techniques. Mean column water velocity ($0.4 \times$ total depth for depths ≤ 0.76 m; 0.2 and $0.8 \times$ total depth for depths > 0.76 m) and velocity at the stream bottom were determined using a Marsh–McBirney model 201 digital flowmeter. Night collections and turbid conditions precluded the measurement of nose depth or nose velocity (Bovee 1986). Substrate composition was classified by size and texture according to a modified Wentworth particle-size scale (Bovee and Milhous 1978).

Suitability Curves

The diel cycle for each species was partitioned into high-feeding and low-feeding periods whenever RWW fell above or below the unweighted (by interval or month) mean RWW (Table 1) in the combined feeding chronology plots (Fig. 2). Separate suitability curves were constructed from physical measurements associated with sites where fish were located during high- and low-feeding periods. Unweighted measurements of depth and velocity were tabulated and grouped into increments of 0.1 m and 0.1 m·s⁻¹, respectively. Substrates were classified into 10 groups ranging in particle size from bed-rock to boulder. In observations of mixed substrate, the prevalent class was used. Frequencies of measurements for each variable were normalized to unity, i.e. the modal range of each habitat parameter was assigned a value of 1.0, and frequencies of other intervals were expressed as a proportion of the mode. Utilization, i.e. the relative frequency of observations for each microhabitat variable (Bovee 1986), was plotted for each variable, and a curve was fitted to the data by interpolation. To facilitate a smooth curve, a range of no use between two ranges of a habitat variable used by a species was not incorporated into the curve. Unweighted frequency distributions of microhabitat use for each species during high-feeding and low-feeding periods were compared using the Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1981) using the same class sizes for habitat variables specified above. Suitability curves and

TABLE 2. Summary of microhabitat use during high-feeding and low-feeding periods by fishes of the Salt Fork and Middle Fork of the Vermilion River, Illinois. Data are total length (TL) ($\pm$ SD), techniques used to locate fish (DO = direct observation, PE = prepositioned electrofishing, RT = radiotelemetry), sample size (number of locations), mean values (and range) of depth and mean and bottom velocity, substrate particle size range, and *D* statistic of Kolmogorov-Smirnov two-sample test comparing microhabitat frequency distributions for each habitat variable during high-feeding and low-feeding periods. Results for common carp are not presented according to feeding regime due to low sample size. Significant *D* values: * $P \leq 0.10$; ** $P \leq 0.05$; *** $P \leq 0.01$.

Species and feeding intensity	Mean TL (mm)	Techniques	<i>N</i>	Habitat variable			
				Depth (m)	Mean velocity (m·s ⁻¹)	Bottom velocity (m·s ⁻¹)	Substrate
Common carp	418 $\pm$ 34	DO	13	0.33 (0.15–0.88)	0.14 (0–0.27)	0.07 (0–0.18)	Silt – fine gravel
Golden redhorse	249 $\pm$ 104	DO, PE, RT	9	0.38 (0.18–0.58)	0.18 (0–0.37)	0.04 (0–0.12)	Bedrock – fine gravel
High feeding			21	0.48 (0.15–1.25)	0.14 (0–0.58)	0.06 (0–0.30)	Bedrock – coarse gravel
Low feeding				0.38	0.24	0.10	0.48*
<i>D</i>							
Channel catfish	415 $\pm$ 42	RT	74	0.79 (0.15–1.71)	0.08 (0–0.55)	0.01 (0–0.09)	Bedrock – small cobble
High feeding			43	0.80 (0.46–1.28)	0.07 (0–0.24)	0.01 (0–0.09)	Bedrock – coarse gravel
Low feeding				0.26*	0.06	0	0.06
<i>D</i>							
Smallmouth bass	275 $\pm$ 53	DO, PE, RT	81	0.57 (0.18–1.25)	0.04 (0–0.58)	0.02 (0–0.12)	Bedrock – small cobble
High feeding			43	0.54 (0.18–1.25)	0.13 (0–0.70)	0.04 (0–0.43)	Bedrock – boulder
Low feeding				0.19	0.32**	0.06	0.22
<i>D</i>							
Longear sunfish	88 $\pm$ 17	DO, PE	82	0.40 (0.12–0.85)	0.05 (0–0.40)	0.02 (0–0.24)	Silt – large cobble
High feeding			18	0.31 (0.21–0.46)	0.04 (0–0.12)	0.01 (0–0.03)	Bedrock – large cobble
Low feeding				0.32*	0.10	0.11	0.38**
<i>D</i>							

comparisons of frequency distributions are not presented for common carp due to limited sample sizes (13 locations total).

Results

Feeding Chronology and Daily Ration

Relative stomach or foregut content wet weights (RWW) varied widely among individuals both within and between sampling intervals for each species, and standard deviations were often greater than mean values (Table 1). Mean daily RWW varied among months and species, ranging from 0.05% for common carp in July to 1.04% for channel catfish in the same month. The stomachless species, common carp and golden redhorse, had low combined mean RWW values of 0.15 and 0.16%, respectively, while higher combined means ranging from 0.65 to 0.68% were found in the fishes with stomachs: channel catfish, smallmouth bass, and longear sunfish.

Significant differences in RWW between sampling intervals for a diel experiment ($P < 0.05$) were detected in common carp, golden redhorse, and channel catfish, indicating discontinuous feeding (Table 1). Common carp and golden redhorse both fed discontinuously in the July and October

experiments, and channel catfish did so in May. Variation in RWW over time appeared high in general diel plots (data for three diel series combined) for all species (Fig. 2), but feeding was discontinuous ($P < 0.05$) only in golden redhorse and channel catfish when combined data were tested, and golden redhorse feeding (as inferred from RWW) declined significantly ($P < 0.01$) from 2300 to 0200 Central Standard Time (CST).

Diel feeding chronologies for common carp and the centrarchid species were similar, suggesting peaks in feeding intensity associated with sunrise and sunset (Fig. 2). Feeding was higher during dark hours for common carp compared with daylight hours and was lower at night for longear sunfish. Golden redhorse feeding decreased sharply after a peak at 2300 CST and then progressively increased through the remainder of the diel series. Channel catfish feeding peaked near sunrise (0500 CST) and was generally high during dark and morning hours and was low during the afternoon and near sunset.

The percentage of empty stomachs in each experiment ranged from 0 for smallmouth bass in May and July to 43.9 for common carp in July and showed a general inverse relationship with mean RWW (Table 1). Percentage of empty stomachs was lowest in October for common carp, golden redhorse, and

channel catfish, but was conversely the highest in that month for the two centrarchid species.

Gastric evacuation rates (R) ranged from $0.09 \cdot h^{-1}$ for common carp in October to $0.32 \cdot h^{-1}$ for smallmouth bass in May and July (Table 1). Estimates of R correlated positively with mean water temperature during an experiment for all species except golden redhorse, where the correlation was negative. Daily ration (C_{24}) estimates were higher in species with stomachs compared with those of species without stomachs and ranged from 0.23% for common carp in May to 7.73% for channel catfish in July. Confidence limits for C_{24} were generally near or below $\pm 50\%$ of the estimate for all species except smallmouth bass, where confidence limits were higher, primarily due to low sample sizes.

Microhabitat Use Associated with Feeding

Fish examined occurred in a diversity of habitats as reflected by the variation in quantitative microhabitat measurements for each species (Table 2; Fig. 3 and 4). Common carp and golden redhorse were found in similar shallow habitats with moderate velocities and a restricted range of fine substrates. Channel catfish occurred in a wide range of habitats deeper than those for other species with low velocities over a wide range of bottom materials, but most frequently over silt-clay. Smallmouth bass and longear sunfish habitats were similar areas of shallow to moderate depth, low velocity, and a wide range of substrate sizes. However, ranges of all habitat variables were wider for smallmouth bass than those for longear sunfish.

Microhabitat use frequency distributions during high-feeding and low-feeding periods were significantly different ($P \leq 0.10$) for at least one habitat variable for each species examined (Table 2), indicating differential habitat use during these periods. Differences were detected in substrate for golden redhorse, depth for a channel catfish, mean velocity for smallmouth bass, and depth and substrate for longear sunfish.

Habitat suitability curves provide a descriptive tool to characterize these differences in habitat use associated with feeding (Fig. 3 and 4). Golden redhorse habitat during high-feeding periods was shallower, lower in velocity, and had finer substrates than during low-feeding periods, and ranges used most frequently (modes) associated with each feeding regime were different for depth and substrate (Fig. 3a). Modal use during high-feeding and low-feeding periods was equivalent for all habitat variables for channel catfish, but ranges of depth, mean velocity, and substrate particle size extended higher during high-feeding hours (Fig. 3b). Smallmouth bass used a similar range of depths in each feeding regime, but the modal range during high-feeding hours was 0.2 m deeper than that during low feeding (Fig. 4a). High-feeding habitat for that species was lower in velocity and had a coarser substrate mode than low-feeding habitat, yet areas over boulders were used only during low-feeding hours. Longear sunfish high-feeding habitat was deeper and swifter than that of low-feeding periods, but the modes during the two regimes were identical (Fig. 4b). Modes of substrate use for the two periods were the same, but longear sunfish were found more frequently over gravel substrates during high-feeding times and used areas with bedrock only during low feeding.

Although statistical comparison is not possible for the data on cover associated with habitat used during low-feeding and high-feeding hours, notable differences were found in the proportions of locations with cover between feeding regimes for all species examined (Table 3). Common carp were associated with branch piles or plants at 69% of locations. Golden redhorse

used woody structure, large rocks, and root wads in equal proportions, but were associated with cover over twice as often during high-feeding periods. The same three cover types were used by channel catfish, but this species was found using tree roots more frequently than other types of cover. Channel catfish used cover more frequently during low-feeding hours. Smallmouth bass were associated with woody structure, large rocks, and roots in equivalently low proportions during high feeding. The species was found using the same cover during low feeding but much more frequently used large rocks and roots. Longear sunfish and common carp were the only species studied that used live vegetation for cover. Cover in the form of woody structure, rocks, plants, and roots was associated with equivalent proportions of longear sunfish habitat during high-feeding hours. This species was found using cover in 100% of locations during low-feeding hours (nearly twice as often as in high-feeding periods) with woody structure used most frequently. Of the vegetation used as cover, aquatic plants were favored by this fish during low-feeding hours and terrestrial plants during high feeding.

Discussion

Comparison of our feeding results with those of other investigators is limited by differences in methodology and units used to express results. Principal differences in methods to determine feeding patterns include variation in the proportion of the alimentary canal sampled (e.g. stomach or foregut versus entire canal), the method of measuring content weight and fish body weight (wet or dry) and the coincidental expression of those weights as a proportion, and the many variations employed to calculate estimates of gastric evacuation rate (R) and daily ration (C_{24}) (Elliot and Persson 1978; Adams and Breck 1990, and papers cited therein).

Furthermore, interpretation of our results is complicated by variable, unequal, and often relatively low sample sizes. We acknowledge these shortcomings and advise caution in interpretation. Thus, the failure to detect statistically significant trends in data may not lead to a definitive conclusion. For example, significant differences among sampling intervals over the diel period indicate that feeding is discontinuous; however, the absence of significance does not necessarily imply continuous feeding unless sample sizes and variability are sufficient to achieve reasonable test power. Another finding where sample size may influence interpretation is the comparison of habitat descriptions stratified by feeding regime. Channel catfish high-feeding habitat was more diverse (wider ranges in variables) than that during low-feeding hours, but this result is confounded with variation in sample size (Table 2; Fig. 3b). However, the demonstration of the reverse trend (wider variation with lower number of samples) in smallmouth bass (Table 2; Fig. 4a) supports the validity of these results as indicating biological differences in habitat use. Such considerations also led us to consider $P \leq 0.10$ statistically significant for the relatively low sample sizes of frequency distributions compared by the Kolmogorov-Smirnov two-sample test (Table 2). Our utilization curves (Fig. 3 and 4) would probably be smoothed further before using them in an instream flow assessment, but we have minimized smoothing to preserve detail in comparisons.

Measurements of microhabitat use of all species we examined (Table 2) conform well to qualitative habitat descriptions found elsewhere (Scott and Crossman 1973; Pflieger 1975; Smith 1979; Becker 1983), and further discussion is presented according to species.

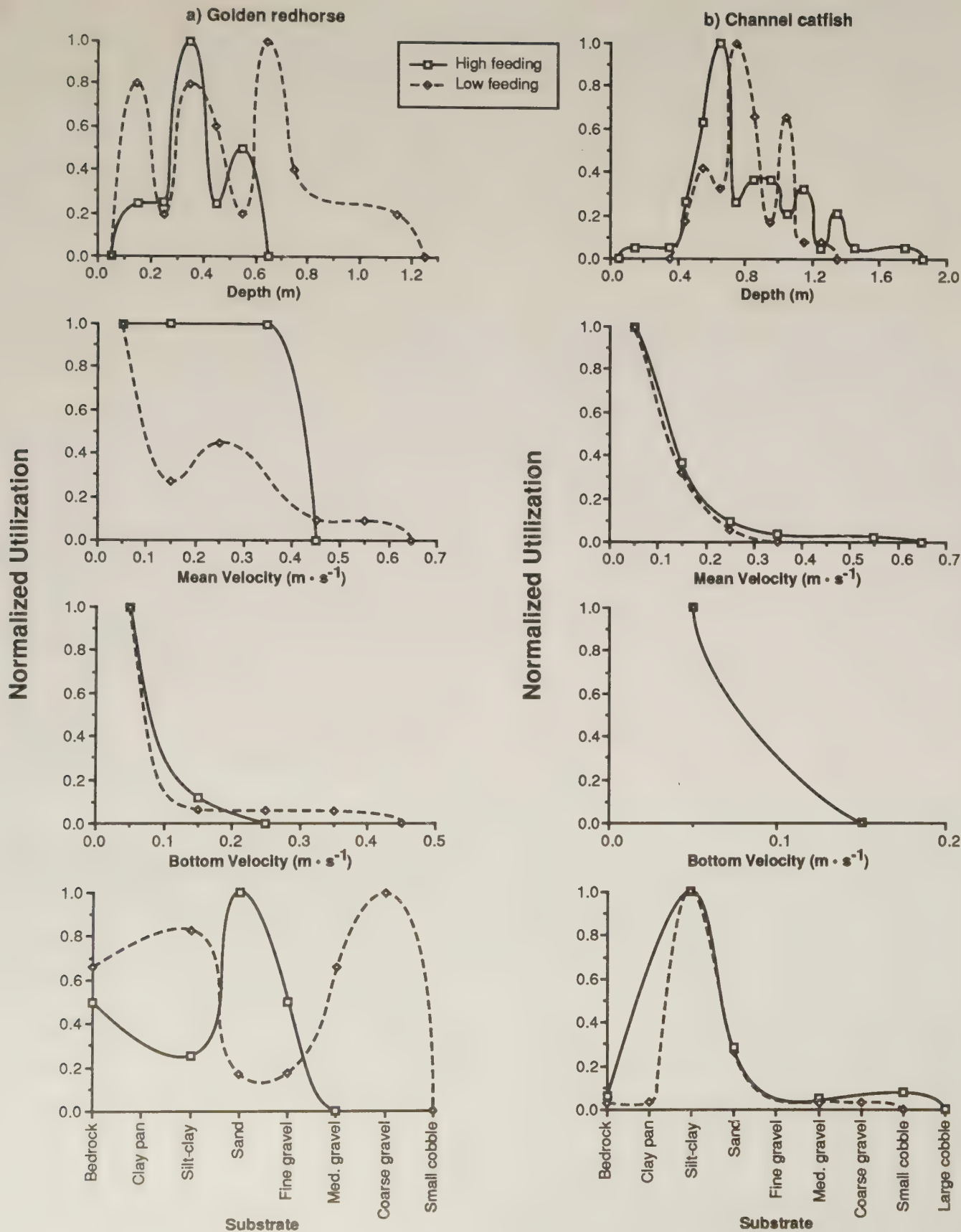


FIG. 3. Microhabitat utilization (frequency of use) curves stratified by feeding regime (high or low) for golden redhorse (left column) and channel catfish (right column) in the Salt Fork and Middle Fork of the Vermilion River, Illinois. Sample sizes (number of locations) are given in Table 3.

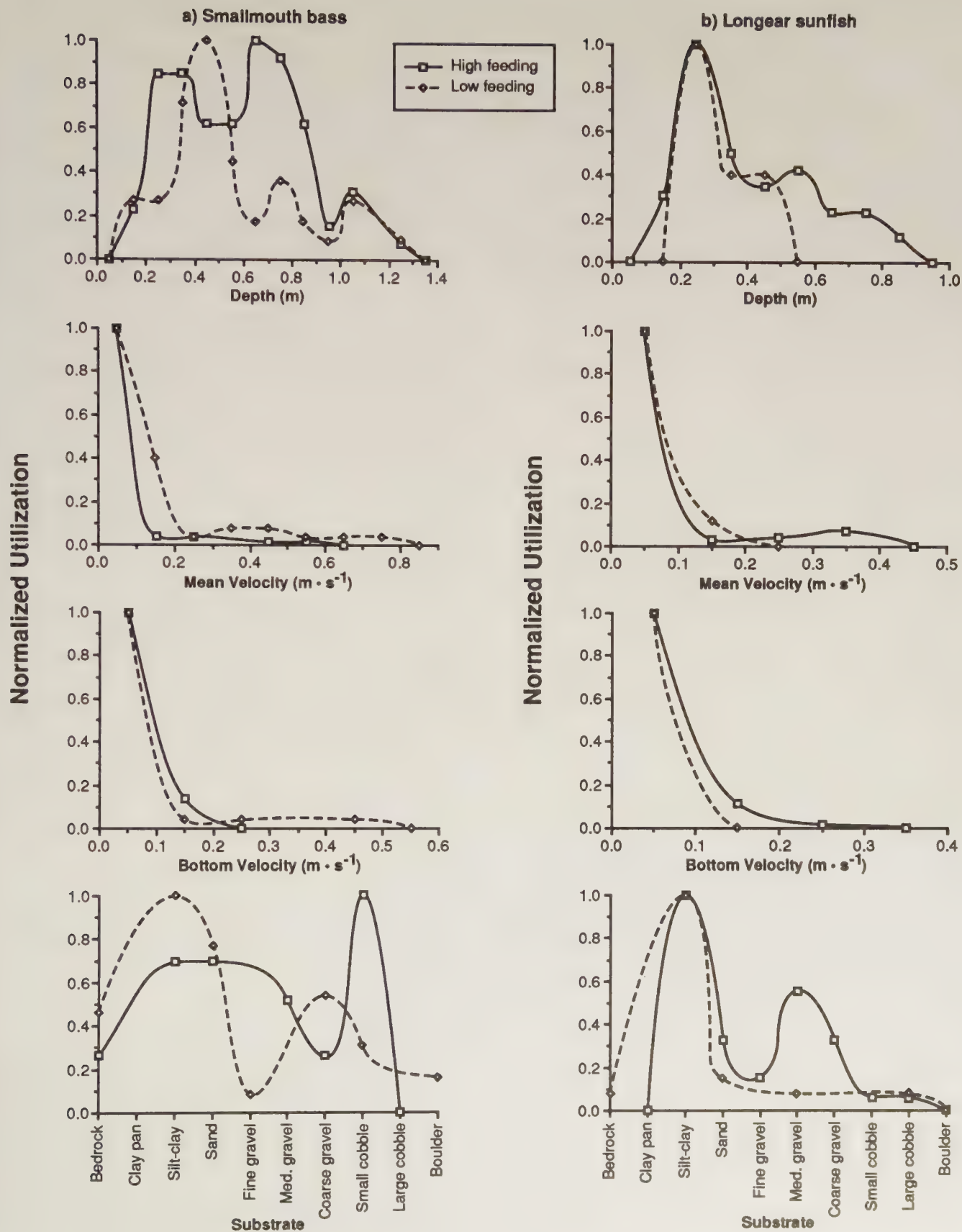


FIG. 4. Microhabitat utilization (frequency of use) curves stratified by feeding regime (high or low) for smallmouth bass (left column) and longear sunfish (right column) in the Salt Fork and Middle Fork of the Vermilion River, Illinois. Sample sizes (number of locations) are given in Table 3.

TABLE 3. Percent by number of microhabitat locations where fishes were associated with cover during high-feeding and low-feeding periods in the Salt Fork and Middle Fork of the Vermilion River, Illinois. Sample sizes are listed in Table 2.

Species and feeding intensity	Cover type					Total
	Woody structure	Large cobble and boulders	Terrestrial plants	Aquatic plants	Root wads	
Golden redhorse						
High feeding	11.1	11.1	0	0	11.1	33.3
Low feeding	4.8	4.8	0	0	4.8	14.3
Channel catfish						
High feeding	8.1	4.1	0	0	28.4	40.5
Low feeding	9.3	4.6	0	0	37.2	51.2
Smallmouth bass						
High feeding	2.5	4.9	0	0	3.7	11.1
Low feeding	4.7	23.3	0	0	18.6	46.5
Longear sunfish						
High feeding	13.4	11.0	13.4	1.2	18.3	57.3
Low feeding	61.1	11.1	0	16.7	11.1	100.0

Common Carp

Statistical analyses of entire gut contents of Mississippi River common carp indicated a uniform pattern of feeding throughout the diel cycle (Garcia and Adelman 1985), in contrast with the discontinuous feeding patterns that we detected in July and October (Table 1). The estimates of R obtained for common carp by Garcia and Adelman (1985) of $0.23\text{--}0.27\cdot\text{h}^{-1}$ at $21.5\text{--}26.5^\circ\text{C}$ and those found in field studies by other stomachless cyprinid fishes (*Pachychilon pictum*, *Leuciscus cephalus*, *Rutilus rubilio*) of $0.22\text{--}0.24\cdot\text{h}^{-1}$ at 25°C (Kitchell et al. 1978) are similar to that found in our July experiment for common carp of $0.25\cdot\text{h}^{-1}$ at a mean temperature of 26.0°C . Lower R values similar to those we calculated for the May and October experiments were reported by Garcia and Adelman (1985) at corresponding temperatures. Methodological differences precluded comparison of C_{24} estimates.

In streams, common carp are usually found in deep pools (Pflieger 1975; Becker 1983); however, all but one microhabitat location for common carp in our study were from the channelized agricultural upstream area of the Salt Fork. These occurrences suggest that this highly adaptable species was exploiting this enriched but severe environment of dramatic fluctuations in temperature and oxygen (Wiley et al. 1990) that less tolerant species could not.

Golden Redhorse

We found no other analogous feeding studies of golden redhorse or other members of *Moxostoma* in the literature. Daily food consumption by young white suckers (*Catostomus commersoni*) calculated by Dobie (1972) ($8.5\text{--}19.0\%$) was much greater than that of golden redhorse in our study ($0.31\text{--}1.22$). The negative relationship between fish size and C_{24} found by Dobie (1972), however, suggests that the disparate findings between studies are due to size effects.

In accord with the positive relationship found between R and water temperature in four of the five species we studied (Table 1), gastric evacuation rate of many other species has shown a positive exponential relationship to temperature (Elliot and Persson 1978; Adams and Breck 1990, and papers cited

therein). The inverse relationship between R of golden redhorse and mean water temperature during each 24-h experiment may indicate a systematic error in methods or could be the result of interseasonal variation in food habits. Golden redhorse R was calculated from intervals during dark hours following a peak in RWW, when no feeding was assumed. We are unable to determine if this assumption was met during the intervals selected, and its violation may account for the unexpected results. Furthermore, behavioral and physiological factors may also have influenced these results, as variation in the size and composition of food items or meal size and frequency can alter digestion rates (Windell 1978; Flowerdew and Grove 1979; Persson 1981; Mills et al. 1984). Ahlgren (1990) found that diet composition of juvenile white suckers in ponds varied significantly with season and with relative availability of food items. The proportion of detritus in white sucker foreguts in that study varied seasonally from 5% in July to 97% in January and February. The food habits of golden redhorse are likely to be equally variable in its dynamic lotic surroundings and could account for the observed variation in digestion from the accepted trend. Considering the equivalent sizes of golden redhorse among experiments (Table 1), size effects probably did not influence estimated R values.

Channel Catfish

In support of the perception of most anglers and the general contention of Pflieger (1975) that channel catfish are inactive during the day and feed at night, Bailey and Harrison (1945) found feeding most active from sunset to midnight, and Davis (1959) also noted nocturnal feeding. Contrary to these conclusions, Mathur (1970) reported feeding greatest during daylight hours, based on mean weights of stomach contents (not expressed as a proportion of fish weight). We also found channel catfish feeding during the day with peaks in feeding near sunrise (0500 CST), midday (1100 CST), and at night (2300 CST), but little feeding occurred through the afternoon (Fig. 2). Channel catfish are omnivorous and opportunistic in their food habits, showing wide variation in diet through the diel period and among seasons (Bailey and Harrison 1945; Mathur 1970).

Our results in comparison with those of these other investigators suggest that the diel feeding chronology of this species is variable as well.

The slightly deeper mode (Fig. 3b) and greater use of cover (Table 3) by channel catfish during low-feeding hours support the habitat aspect of Davis' (1959) findings that adults spend the day in deep holes, under logs or other shelter, and feed in shallow water at night. The wider range of depth and substrate size that we found during high-feeding periods may indicate movement between habitats during these hours. Confirming the finding that channel catfish seldom occur in dense aquatic vegetation (Trautman 1981), woody structure, rocks, and roots were the only forms of cover used by this species in our study.

Smallmouth Bass

Smallmouth bass RWW variation was wide among individuals within a sampling interval; nonetheless, peaks near sunrise and sunset were evident in the feeding chronology (Fig. 2). A similar diel feeding pattern was described by Hubbs and Bailey (1938) and was demonstrated for young smallmouth bass collected in August by Stewart (1978). Laboratory studies also confirmed diurnal feeding (Munther 1970). The daily ration estimate of 4.2%, calculated for young smallmouth (Stewart 1978) using the method of Keast and Welsh (1968), which is considered a minimal estimate, fell within the seasonal range of 3.17–6.05% for juvenile and adult smallmouth bass in our study (Table 1). The ranges of mean RWW of stomach contents (0.36–1.14%) and percent empty stomachs (0–38%) determined in seasonal feeding studies of juvenile and adult largemouth bass (*Micropterus salmoides*) by Cochran and Adelman (1982) contain the corresponding ranges that we determined for smallmouth bass (0.62–0.82% mean RWW and 0–20.5% empty). However, daily rations that we calculated for smallmouth bass (3.17–6.05%) are slightly higher than those of largemouth bass (1.19–5.58%), due in part to relatively higher *R* values that we estimated for smallmouth bass. *R* estimates calculated from mean temperatures during each of our diel experiments using an exponential function derived by Cochran and Adelman (1982) for largemouth bass were 0.07, 0.21, and 0.05·h⁻¹ for May, July, and October, respectively, as compared with 0.32, 0.32, and 0.20·h⁻¹ calculated in our study. The reasons for the interspecific differences in *R* may be methodological, behavioral, or physiological as discussed above for golden redbreast.

The habitat use that we determined for smallmouth bass (Fig. 4a) corresponds well with other relationships developed from field observations (Orth et al. 1982; Rankin 1986) and laboratory simulation (Sechnick et al. 1986). Although this species is typically associated with coarse rocky substrates (Reynolds 1965; Munther 1970; Orth et al. 1982; Paragamian 1981; Rankin 1986), Vermilion River smallmouth bass frequently occurred over fine substrates (Fig. 4a). In contrast with laboratory experiments (without prey present) where smallmouth bass showed no substrate preference, habitat choice of stream-dwelling fish was influenced by depth, velocity, and strongly by substrate (Sechnick et al. 1986; Rankin 1986). These disparate findings between laboratory and natural environments suggest that selection for large-diameter substrates by smallmouth bass in a natural stream may be a response to variability in velocity caused by irregular substrates (Hynes 1970; Rankin 1986) or to cover (Rankin 1986; Sechnick et al. 1986), but are most likely due to differences in prey densities (deMarch 1976; Stein 1977; Minshall 1984; Rankin 1986).

High-feeding habitat of smallmouth bass had significantly lower velocities than those found during low feeding (Table 2), a result that supports the characterization of this species feeding in quiet areas along the shoreline (Pflieger 1975). During low-feeding hours, fish occurred in higher velocities, but more frequently used cover, presumably as a shelter from flow (Table 3; Fig. 4a). Other studies also demonstrated the importance of cover as a habitat determinant for smallmouth bass (Munther 1970; Probst et al. 1984; McClendon and Rabeni 1987). While we did not detect a significant difference in substrate selection between feeding regimes of smallmouth bass, the modal substrate classes are distinct (Table 2; Fig. 4a). We found smallmouth bass most frequently over coarse substrates (small cobble) during high-feeding periods, similar to observations by Rankin (1986) of foraging occurring primarily over boulder, rubble, and cobble substrates. Moreover, smallmouth bass habitat use during feeding may be influenced by associations with other species such as suckers (Catostomidae) or turtles (Pflieger 1975; Rankin 1986); however, we are unable to address this relationship.

Longear Sunfish

Feeding studies of longear sunfish are rare, but many have been conducted on other centrarchid species, with studies of bluegill (*Lepomis macrochirus*) being most numerous. Similar to our findings for longear sunfish (Fig. 2), bluegill feeding is primarily diurnal with an occasional nocturnal component (Keast and Welsh 1968; Baumann and Kitchell 1974; Sarker 1977). Studies of other sunfishes including pumpkinseed (*L. gibbosus*) (Keast and Welsh 1968), white crappie (*Pomoxis annularis*) (Childers and Shoemaker 1953; Mathur and Robbins 1971), and black crappie (*P. nigromaculatus*) (Childers and Shoemaker 1953; Keast 1968) found a similar pattern of diurnal feeding, often with peaks near sunrise or sunset. Becker (1983) noted that longear sunfish become inactive at night, but feeding may occur under bright moonlight.

Despite a negative correlation of longear sunfish density in lakes with percent cover, Laughlin and Werner (1980) found highest densities in areas of moderate cover. Longear sunfish in the Vermilion River were strongly associated with cover, particularly during low-feeding periods (Table 3), but utilized the open, deeper, and swifter waters over coarse substrates of the stream channel during feeding. Studies of bluegill suggest that such a pattern of habitat use is a response to the presence of predators and that sunfish sacrifice energy gain for safety (Mittelbach 1986, and papers cited therein).

Longear sunfish in our study showed a decline in mean RWW and daily ration and an increase in the percentage of empty stomachs from May to October (Table 1). The same general decreasing seasonal trend has been observed for longear sunfish (Laughlin and Werner 1980; Angermeier 1985), other sunfishes (Seaburg and Moyle 1964; Kitchell 1970; Angermeier 1985), and six other stream fishes (Angermeier 1985). A marked decline in the abundance of invertebrates through the summer in a small stream within the Vermilion watershed was documented by Angermeier and Carlson (1985). The daily ration estimates of Seaburg and Moyle (1964) for three sunfish species (0.58–2.20%), minimum estimates for bluegill (2.5%) and pumpkinseed (2.6%) of Keast and Welsh (1968), and monthly means for bluegill (0.36–2.31%) of Kitchell (1970) were all generally lower than our estimates for longear sunfish (2.00–3.81%). Our daily ration estimates for longear sunfish are all below maximum daily ration estimates for bluegill at equivalent temperatures (Kitchell 1970), but the daily ration for longear

sunfish in May (3.81%) was equivalent to the maximum for bluegill at 15°C (3.86%). These findings indicate that longear sunfish feed near maximum intensity in May, and similar seasonal feeding trends observed for longer sunfish and other species support the hypothesis that invertebrate availability is near maximum for many fish during spring and early summer and decreases through autumn. Alternate feeding strategies by other species that we studied may account for the absence of a similar trend in those fishes.

Recommendations

The findings of this study demonstrate differences in microhabitat use associated with feeding activity for each species examined. By directly observing brown trout (*Salmo trutta*) occurrence during four different activities (including feeding and resting) during daylight hours, Gosse and Helm (1982) also demonstrated significant differences in microhabitat use among activities for all life stages. Distinct and in some cases significantly different habitat use in certain habitat variables may indicate those proximate environmental cues that fish use to distinguish feeding and resting sites. However, the primary stimulus of microhabitat selection in feeding may not be determined from field data because current velocity and substrate are confounded variables in a natural system (higher velocities are associated with coarser substrates). Furthermore, other studies have demonstrated that fish respond to a composite of habitat conditions rather than to a single habitat variable independently (Bain et al. 1988; Orth and Maughan 1982; Moyle and Baltz 1985), and a recent focus on the complexities of hydraulic stream ecology (Statzner et al. 1988; Heede and Rinne 1990) will likely lead to a more realistic multivariate approach to describing habitat use, availability, and quality.

Our results imply that realism could be improved in instream flow assessments if habitat suitability criteria were stratified by feeding regime; however, difficulties involved in such disaggregations should not be overlooked. Diel feeding chronologies are highly variable, reflecting innate behavioral adaptations, flexible behavioral responses to energetic parameters, and responses to competitors and predators. For example, it is well known that many riverine fishes may move between a foraging site and a nearby cover-associated resting site repeatedly while feeding. This type of habitat use within a feeding interval would not be adequately represented in the type of analysis we have employed here. Even with such difficulties, we found clear distinctions in habitat use associated with feeding, and these differences may appear more extreme if habitat availability were considered. Unlike the Vermilion River drainage, many lowland rivers have well-developed fringing floodplains which greatly increase habitat diversity, and the distinction between feeding and resting habitat may also be more evident in such environments. Although admittedly less precise than directly observing fish behavior, the approach that we have adopted here (temporal stratification) allows the distinction of activity in turbid waters and at night when observations are impossible.

An alternative approach to identify and protect feeding habitat of fish is to develop habitat suitability criteria for prey taxa. Orth (1987) discussed the rationale for including aquatic invertebrates and forage fishes in instream flow assessments, and Statzner et al. (1988) have reviewed a variety of such techniques and studies. While this approach may require less field work than conducting a procedure similar to that in our study, sorting and classifying organisms would be labor-intensive in the laboratory. Distinct suitability criteria would have to be developed for each individual (or dominant) prey taxa, and thus

the procedure may be impractical for fishes with diverse or variable food habits. Feeding habitat suitability criteria derived from fish behavior may therefore provide a more realistic composite of optimal prey conditions than those directly obtained for prey. In addition, effort can be reduced if the diel feeding chronology of a fish has revealed a distinct rhythm. In such a case, on-site feeding studies may not be necessary to temporally stratify fish microhabitat use by feeding regime. In a decision between these two approaches, the behavior of both predator and prey must be considered.

Habitat suitability criteria are usually distinguished by species and life stage, and additional stratification by activity or season may also be desirable. Spawning suitability criteria are often developed separately, and our results indicate that distinct criteria for feeding and resting habitat are warranted as well. Gathering frequency data to develop site-specific suitability criteria is costly and labor-intensive and may be limited by economic and logistic constraints. As a pool of data is further stratified, sample size of each suitability function is reduced, and the potential for bias is increased. Bovee and Cochauner (1977) recognized sample size and source of the data in development of evaluation criteria for suitability functions, which were classified into one of four classes ranging from "reconnaissance grade," based only on stream descriptions, to "excellent," requiring a minimum of 200 measurements of occurrence. Practical constraints may limit sample size and the degree of stratification allowed and may thus lead to overlooking a critical habitat. For example, further disaggregation of our habitat use data by season would have provided added insight, but was constrained by sample size. Our objectives in this study were to examine microhabitat use associated with diel feeding chronology; however, seasonal patterns should be addressed in other studies.

There are no standardized procedures for stratifying suitability data, but a bimodal or polymodal habitat frequency distribution may indicate that more than one activity is represented and further stratification may be warranted (Bovee 1986). If activity is not considered, the habitat of a critical activity (e.g. feeding or spawning) will not be adequately represented, and any measurement of central tendency (e.g. mean, median, mode) will be biased toward the predominant activity. The investigator is therefore faced with a subjective decision in balancing sampling bias and realism in determining an optimum level of stratification with limited sample sizes, and fish behavior rather than budgetary concerns should govern this decision. Because most habitat suitability field data are collected during daylight hours, they are variably biased with respect to feeding regime. As a final recommendation, we suggest that when stratification of site-specific suitability data by feeding regime or any other activity is not feasible, field measurements should be collected throughout the diel period under a variety of hydraulic conditions and over several seasons and should include cover associations to minimize bias.

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Profundal Sediment Organic Content and Physical Character Do Not Reflect Lake Trophic Status, but Rather Reflect Inorganic Sedimentation and Exposure¹

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Rowan, D. J., J. Kalff, and J. B. Rasmussen. 1992. Profundal sediment organic content and physical character do not reflect lake trophic status, but rather reflect inorganic sedimentation and exposure. *Can. J. Fish. Aquat. Sci.* 49: 1431–1438.

An analysis of profundal sediment data from 83 north-temperate lakes shows that increasing inorganic sedimentation and exposure (or lake surface area) results in lower organic content and water content, and greater bulk density. Because sedimentation rates are unavailable for most lakes, we estimate sedimentation rates from readily available catchment sediment loads using a mass-balance model. The mass-balance estimate of sediment retention (per square metre of depositional zone) is an excellent predictor of measured inorganic sedimentation rates for a data set covering 19 lakes ($R^2 = 0.92$). Multiple regressions are used to predict organic content, water content, and bulk density of profundal sediment from inorganic sedimentation rates and either exposure or lake surface area, which are surrogates for the energy of the depositional environment. These analyses explain 76, 74, and 66% of the between-lake variation in the three sediment parameters, respectively. Sediment organic content is not related to lake trophic status (chlorophyll *a*) and is negatively correlated with net organic matter sedimentation rates. The common occurrence of organic-rich sediments in oligotrophic shield lakes is, therefore, not a reflection of high organic matter inputs, but rather the extremely low inputs of mineral sediments to these lakes.

Une analyse des données relatives aux sédiments profonds de 83 lacs de la zone tempérée nord a montré que l'accroissement de la sédimentation inorganique et du degré d'exposition (ou de la superficie du lac) se traduisaient par une baisse de la teneur en matières organiques et en eau et une augmentation de la masse volumique générale. Les taux de sédimentation de la plupart des lacs étant inconnus, nous les avons estimés à partir des charges sédimentaires du bassin versant traitées par modèle de bilan massique. L'estimation par bilan massique de la rétention des sédiments (par mètre carré de zone de sédimentation) s'est avérée un excellent facteur de prévision des taux de sédimentation inorganique dans les cas d'un ensemble de données représentant 19 lacs ($R^2 = 0,92$). Des régressions multiples ont été utilisées pour prévoir la teneur en matières organiques, la teneur en eau et la masse volumique générale des sédiments profonds à partir des taux de sédimentation inorganique et du degré d'exposition ou de la superficie du lac, qui remplacent ici l'énergie du milieu de sédimentation. Ces analyses permettent d'expliquer, respectivement, 76, 74 et 66 % de la variation entre lacs de ces trois paramètres sédimentaires. La teneur en matières organiques des sédiments n'est pas liée à l'état trophique du lac (chlorophylle *a*) et présente une corrélation négative avec les taux nets de sédimentation des matières organiques. La présence de sédiments riches en matières organiques dans les lacs oligotrophes du bouclier ne reflète donc pas un apport élevé en matières organiques, mais plutôt un apport extrêmement faible en matières sédimentaires inorganiques.

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Attempts to explain the large between-lake variation in organic content and water content of profundal sediments have not yielded conclusive results. For example, several authors have found positive relationships between lake trophic status and sediment organic content (Rybak 1969; Flannery et al. 1982). However, other authors report little or no correlation between lake trophic status and sediment organic content (Gorham et al. 1974; Håkanson 1984; Rowan and Kalff 1992). Some authors have proposed that inorganic sedimentation dilutes sedimenting organic matter and that the rate of inorganic sedimentation determines both the organic content and

water content (Brunskill et al. 1971; Dean and Gorham 1976; Gorham and Sanger 1976; Brenner and Binford 1988; Rowan and Kalff 1992).

This hypothesis is difficult to test directly because inorganic sedimentation rates have not been calculated for most lakes. However, in principle, sedimentation rates can be estimated from catchment sediment loads using mass-balance models (O'Connor 1988). Catchment sediment loads are routinely monitored at many points in most North American drainage systems. If this can be done with reasonable precision, then the inorganic sediment "dilution" hypothesis may be tested on a large data set.

We use the inorganic sedimentation rates (ISR_{pred}) predicted from the model developed from 19 lakes to test the hypothesis that an increase in inorganic sedimentation rate produces profundal sediment with lower inorganic content and water con-

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tent, and greater bulk density. To do this, we collected sediments from 32 lakes and augmented this with data from the literature for another 51 lakes.

With increasing energy in the depositional environment, one may also expect that profundal sediments will have lower organic content and water content, and greater bulk density. The data set was restricted to sediments at maximum lake depth because maximum depth represents the environment with least energy and where slope effects on sediment texture are usually negligible (Håkanson 1977; Rowan et al. 1992). We also restricted the data set to lakes in which maximum depth exceeds the deposition boundary depth (Rowan et al. 1992). Although wave energy below the deposition boundary depth is not sufficient to move fine particles (Rowan et al. 1992), wind-generated currents of sufficient magnitude to resuspend profundal sediments have been observed in some small lakes (Lemmin and Imboden 1987). Exposure or lake area should, therefore, be a good surrogate for current energy in the depositional environment.

Depth is tested as a surrogate for the decomposition of sedimenting organic matter, as we hypothesize that organic content and water content could be lower in deep lakes.

Finally, we examine the hypothesis that lake trophic status (expressed as mean growing season chlorophyll *a*) can have an important effect on the character of profundal sediment. Multiple regression analysis on basin-averaged variables was used to test all hypotheses.

Methods

Sediments were sampled with a light-weight gravity corer at maximum depth in 32 Quebec and Ontario lakes (Table 1). The surficial 2 cm of sediment was extruded from the 5–10 replicate cores at each site. Sediment water content (percentage of wet weight) was determined by drying at 60°C (Håkanson and Jansson 1983), organic content (percentage of dry weight) was determined by ashing dry sediment at 550°C (Håkanson and Jansson 1983), and bulk density was determined by the syringe method (Hilton et al. 1986).

A literature-based data set of 51 lakes was also compiled (Table 2). This data set was restricted to regions where we could obtain estimates of either river and stream mean suspended sediment concentrations, or lakes for which catchment inorganic sediment loads have been published. For each of the lakes, we were able to obtain at least one of the sediment parameters.

Sediments from 19 lakes were sampled at intervals similar to our field data (0–1, 0–2, or 0–3 cm). Several other authors, however, sampled sediments to a much greater core depth. These include sediments sampled at seven lakes from 0 to 5 cm (Forbes and Hickman 1981; Kelly and Hite 1981), six lakes from 0 to 10 cm (Adams and Duthie 1976; Dean and Gorham 1976; Keulder 1982), and 19 lakes from 0 to 20 cm (Brunskill et al. 1971; Johnson et al. 1986). Sediment texture is known to change with core depth due to the decomposition of organic matter, compaction, and other diagenetic effects; therefore, the differences in sampling interval may have introduced some bias in the analysis. Based on our work, we think that sediments sampled from the surficial 5 cm are reasonably comparable, but that if bias is significant, this would be most notable in sediments sampled from either the 0–10 or 0–20 cm core depths. To test for this potential bias, we created a categorical variable in our multiple regressions by assigning 0 to sediments sampled within the upper 5 cm and 1 to sediments sampled to a greater depth.

For seven of the lakes, only sediment organic carbon content was reported (Thomas et al. 1973; Kemp et al. 1978; Allan 1979; Dominik et al. 1981; Vernet et al. 1984; Thomas 1988). Sediment organic carbon content was converted to organic content by multiplying by 2.13, a factor determined from the relationship of organic carbon and organic content of profundal sediments from 46 Minnesota lakes (Dean and Gorham 1976).

To estimate inorganic sedimentation rates from catchment inorganic sediment loads (Rowan and Kalff 1992), both sediment focusing and through-flow of particles must be taken into account. Therefore, we estimated the inorganic sedimentation rate (grams per square metre per year) as

$$(1) \text{ISR}_{\text{est}} = (\text{CISL} \cdot \text{SRC}) / (\text{SA} \cdot \text{DZ})$$

where CISL is the estimated catchment inorganic sediment load (grams per year) (Rowan and Kalff 1992), SRC is the sediment retention coefficient (O'Connor 1988), SA is the lake surface area (square metres), and DZ is the fraction of the lake comprising the deposition zone (Rowan et al. 1992). When not directly measured, the catchment inorganic sediment load was estimated as

$$(2) \text{CISL} = [\text{SED}] \cdot \text{RO} \cdot \text{DCA}$$

where [SED] is the local mean inorganic suspended sediment concentration (grams per cubic metre) of incoming stream water obtained from government sources (Quebec Ministère des Richesses Naturelles 1970, 1971; Great Lakes Basin Commission 1975; Ontario Ministry of the Environment 1978, 1979; Environment Canada 1985), RO is the annual runoff (metres per year), and DCA is the direct catchment area (square metres), which excludes upstream lakes and their catchments. The sediment retention coefficient was estimated as (O'Connor 1988)

$$\text{SRC} = (\text{WRES} \cdot \text{SV} / h_{\text{mean}}) / (1 + (\text{WRES} \cdot \text{SV} / h_{\text{mean}}))$$

where WRES is the lake water residence time (days), SV is the particle settling velocity (metres per day), and h_{mean} is the mean depth of the lake (metres).

Organic matter sedimentation rates (OSR_{pred}) were estimated from predicted inorganic sedimentation rates (ISR_{pred}) and surficial sediment texture as $\text{ISR}_{\text{pred}} \cdot \text{inorganic fraction}^{-1} \cdot \text{organic fraction}$.

Sedimentation rates (grams per square metre per year) determined from either the Ambrosia horizon, ^{210}Pb , or ^{137}Cs were obtained from the literature for 19 of the lakes (Tables 1 and 2). For 10 of these lakes (Kemp et al. 1974; Robbins and Edgington 1975; Kemp and Harper 1976; Kemp et al. 1977; Kemp et al. 1978; Evans et al. 1981; Evans and Rigler 1983; Dominik et al. 1984; Vernet et al. 1984) the sedimentation rate was measured at more than one site within the depositional zone, and in these instances, the several estimates were averaged. Inorganic and organic sedimentation rates were calculated by multiplying sedimentation rates by the fraction of inorganic or organic matter in the surficial sediments, respectively.

Exposure (square kilometres), the circular integral of fetch (Rasmussen 1988), describes the area exposed or visible from a site and was determined from maps. In several studies, site location was not given (Dean and Gorham 1976; Kelly and Hite 1981; Smith 1983) and exposure could not be determined. Lake surface area (square kilometres), however, was available for all lakes. Therefore, we tested both lake surface area and exposure as surrogates for the energy of the depositional environment. When lake morphometry is simple, exposure and surface area are virtually identical.

TABLE 1. Organic content (OC), water content (WC), bulk density (BD), maximum depth ($h_{\max}$), lake surface area (SA), exposure (E), estimated inorganic sedimentation rate (ISR_{est}), and predicted inorganic sedimentation rate (ISR_{pred}) for 32 Quebec and Ontario lakes sampled at maximum depth.

Lake	OC (% dry wt)	WC (% wet wt)	BD ($\text{g}\cdot\text{mL}^{-1}$)	$h_{\max}$ (m)	SA (km^2)	E (km^2)	ISR_{est} ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	ISR_{pred} ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)
<i>Southern Ontario</i>								
Anstruther	29.9	94.5	1.023	43	6.34	3.00	2	27
Bay	31.5	96.3	1.030	23	1.63	1.50	1	19
Koshlong	41.9	96.0	1.046	43	4.01	2.33	3	34
Long	51.7	99.3	1.064	23	1.17	0.33	2	27
Loucks	50.9	97.5	1.021	18	0.37	0.33	1	20
L'Amable	33.2	95.9	1.040	37	1.78	1.68	4	41
Salmon	56.3	97.3	1.038	31	1.72	1.35	3	36
Stony	58.2	95.0	1.066	29	30.73	5.35	6	48
Wolf	54.4	97.2	1.036	9	1.20	0.68	1	23
<i>Quebec Shield</i>								
Demarest	43.8	96.6	1.044	8	0.06	0.06	8	55
Franciscains	43.5	94.8	1.020	15	0.09	0.09	12	69
Loutre	45.7	96.5	1.023	17	0.59	0.59	5	46
Pyrolle	44.2	94.2	1.040	9	0.08	0.08	17	79
<i>Eastern Townships, Quebec</i>								
Brome	19.8	91.6	1.086	13	14.52	13.95	209	253
Bromont	13.1	83.9	1.185	7	0.47	0.47	650	427
Brompton	20.0	90.9	1.070	42	11.91	8.14	80	163
Coulombe	30.2	92.3	1.077	12	0.67	0.67	242	271
Drolet	22.7	92.8	1.051	7	2.85	1.72	60	143
D'Argent	20.4	86.2	1.086	16	1.04	1.04	279	289
Hertel	32.2	95.6	1.031	8	0.33	0.33	169	230
Leclerc	27.0	91.1	1.072	7	0.05	0.05	5	47
Lovering	15.3	87.7	1.116	25	4.64	2.47	114	192
Orford	23.8	91.3	1.082	48	1.22	1.03	93	175
O'Malley	31.0	96.3	1.048	13	0.16	0.16	61	144
Roxton	27.6	90.0	1.067	6	1.93	1.93	190	242
Waterloo	33.1	94.2	1.064	5	1.50	1.30	279	289
<i>Lake Memphremagog, Quebec-Vermont</i>								
Fitch Bay	23.3	94.4	1.049	18	2.80	5.26	15	76
Sargent Bay	21.1	91.3	1.045	38	4.18	6.13	78	161
South Basin	11.0	82.6	1.112	11	41.92	33.52	298	298
North Basin	17.2	89.4	1.096	29	19.35	22.29	38	115
<i>Lake Ontario, Ontario - New York</i>								
Niagara Basin ^a	14.9	83.9	1.123	244	19 019	17 117	830	477
<i>Lake Erie, Ontario - New York</i>								
Eastern Basin ^a	8.6	73.6	1.209	64	25 220	23 202	1091	541

^aObserved inorganic sedimentation rates are $386 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for the Niagara Basin of Lake Ontario (Kemp et al. 1974; Kemp and Harper 1976) and $1225 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for the Eastern Basin of Lake Erie (Kemp et al. 1977).

Mean growing season chlorophyll *a* concentrations (milligrams per litre) were obtained from Rasmussen (1988), Janus and Vollenweider (1981), Watson et al. (1976), Tarapchak and Stoermer (1976), and open files of both the Ontario Ministry of Natural Resources and the Quebec Ministère des Richesses Naturelles.

Results

Predicting Inorganic Sedimentation Rates (ISR)

ISRs obtained from the literature (Tables 1 and 2) for 19 lakes were regressed against ISR_{est} (eq. 1) and were highly positively correlated ($R^2 = 0.92$, $\text{SE}_{\text{est.}} = 0.151$) (Fig. 1):

$$(3) \log \text{ISR}_{\text{pred}} = 0.460(0.033) \log \text{ISR}_{\text{est}} + 1.337(0.068).$$

The explained variation (92%) is high considering that these data span almost the entire size and depth range for lakes (Tables 1 and 2), but the slope of the relationship is significantly less than 1. For lakes with ISRs of less than about $150 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, ISR_{est} (eq. 1) are considerably lower than observed rates. Davis and Ford (1982) found in Mirror Lake (ISR of $109 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) that more than 71% of the ISR is attributable to dissolved silica sedimented as diatom frustules. At the opposite extreme, Lakes Geneva and Constance have ISRs much lower than estimates due to deltaic sedimentation (Dominik et al. 1981; Vernet et al. 1984). Lakes with ISRs from 150 to $300 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ have

TABLE 2. Organic content (OC), water content (WC), bulk density (BD), maximum depth ($h_{\max}$), lake surface area (SA), exposure (E), estimated inorganic sedimentation rate (ISR_{est}), predicted inorganic sedimentation rate (ISR_{pred}), and observed inorganic sedimentation rate (ISR) at maximum depth of 51 lakes.

Lake	OC (% dry wt)	WC (% wet wt)	BD ($\text{g}\cdot\text{mL}^{-1}$)	$h_{\max}$ (m)	SA (km^2)	E (km^2)	ISR_{est} ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	ISR_{pred} ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	ISR ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)
<i>New Hampshire^a</i>									
Mirror	33.0	87.0		11	0.15	0.14	18	81	109
<i>Northern Illinois^b</i>									
Bangs	19.9			8	1.20		158	222	
Cedar	10.2			12	1.15		121	197	
Crystal	10.5			13	0.92		608	414	
Diamond	13.7			7	0.60		132	205	
Long	13.1			9	1.36		299	298	
Round	15.5			11	0.87		114	191	
<i>Northeastern Minnesota^c</i>									
Crane	16.9			24	12.50		18	82	
Iron	40.2			6	0.42		2	29	
Kimball	46.9			6	0.32		2	31	
Wilson	17.4			14	2.47		3	38	
<i>Laurentian Great Lakes, Ontario-USA^d</i>									
Georgian Bay	6.6	80.2	1.135	165	15 111	24 242	11	67	54
Huron	9.1	80.5	1.132	226	40 509	41 843	93	175	274
S. Huron	9.6	71.5		110	40 509	36 804	322	309	294
Michigan	10.1	81.0	1.110	281	58 016	47 468	165	230	151
Superior	8.3	81.5	1.125	406	82 376	53 442	138	209	138
<i>Western Ontario^e</i>									
ELA 114	58.5	96.2		5	0.12	0.11	22	90	
ELA 122	40.2	93.8		13	0.12	0.12	21	87	
ELA 132	48.8	95.9		8	0.07	0.06	14	73	
ELA 227	48.5	95.8		10	0.05	0.05	37	114	
ELA 230	62.4	96.9		14	0.02	0.02	9	58	
ELA 239	24.0	90.7		30	0.56	0.50	15	76	
ELA 240	29.8	91.9		13	0.44	0.43	13	70	
ELA 241	59.4	95.8		13	0.02	0.02	55	137	
ELA 261	42.1	95.8		10	0.06	0.06	27	99	
ELA 265	43.5	95.4		19	0.13	0.13	14	72	
ELA 302	31.7	94.6		14	0.24	0.13	12	69	
ELA 303	58.4	96.2		3	0.10	0.10	30	103	
ELA 304	50.7	96.8		7	0.04	0.04	31	106	
ELA 305	24.0	89.9		33	0.52	0.50	11	66	109
<i>Central Ontario^f</i>									
L. Batchwana	50.0	93.4	1.041	11	0.06	0.05	8	55	35
U. Batchwana	49.0	93.6	1.040	11	0.06	0.05	3	37	
Turkey	28.0	90.6	1.060	37	0.52	0.37	3	38	50
L. Turkey	37.0	93.4	1.041	13	0.19	0.19	4	40	35
Wishart	42.0	94.5	1.034	5	0.19	0.17	9	59	48
<i>Southern Ontario^g</i>									
Blue Chalk	35.0	92.8	1.046	23	0.49	0.29	2	29	
Chub	45.0	93.3	1.042	27	0.32	0.30	6	48	
Clear	40.0	92.5	1.047	33	0.88	0.62	1	21	
Costello	36.8	94.9		18	0.34	0.28	11	65	69
Crosson	44.0	92.3	1.048	25	0.57	0.57	6	48	
Dickie	37.0	92.5	1.047	12	0.93	0.84	3	37	
Heney	39.0	93.0	1.044	6	0.19	0.19	3	33	
Jerry	40.0	92.2	1.049	35	0.50	0.40	10	63	
Plastic	46.0	92.6	1.046	16	0.32	0.29	2	29	
Red Chalk	42.1	98.2		38	0.44	0.43	3	38	38
Sunfish	11.3	92.6	1.130	20	0.08	0.08	146	215	212

TABLE 2. (Concluded)

Lake	OC (% dry wt)	WC (% wet wt)	BD (g·mL ⁻¹)	$h_{\max}$ (m)	SA (km ²)	E (km ²)	ISR _{est} (g·m ⁻² ·yr ⁻¹)	ISR _{pred} (g·m ⁻² ·yr ⁻¹)	ISR (g·m ⁻² ·yr ⁻¹)
<i>Alberta^b</i>									
Hastings	27.0	85.0		8	8.44	5.61	21	88	83
<i>Northwest Territoriesⁱ</i>									
Great Slave	3.0			614	28 600	16 913	9 137	1 439	
<i>Europe^j</i>									
Constance	5.7	77.0	1.157	252	540	446	5 919	1 178	982
Geneva	6.8	82.6	1.113	310	580	508	11 087	1 573	1 491
<i>South Africa^k</i>									
Wuras	12.5			5	0.67	0.55	60 015	3 419	

^aVon Damm et al. (1979) and Davis and Ford (1982).

^bKelly and Hite (1981).

^cDean and Gorham (1976).

^dThomas et al. (1973), Robbins and Edgington (1975), Torrey (1976), Kemp and Harper (1977), Kemp et al. (1978), Robbins (1980), Evans et al. (1981), and Thomas (1988).

^eBrunskill et al. (1971) and Brunskill and Schindler (1971).

^fJohnson et al. (1986).

^gAdams and Duthie (1976), Evans and Rigler (1983), and Smith (1983).

^hForbes and Hickman (1981).

ⁱRawson (1950) and Allan (1979).

^jDominik et al. (1981, 1984) and Vernet et al. (1984).

^kKeulder (1982).

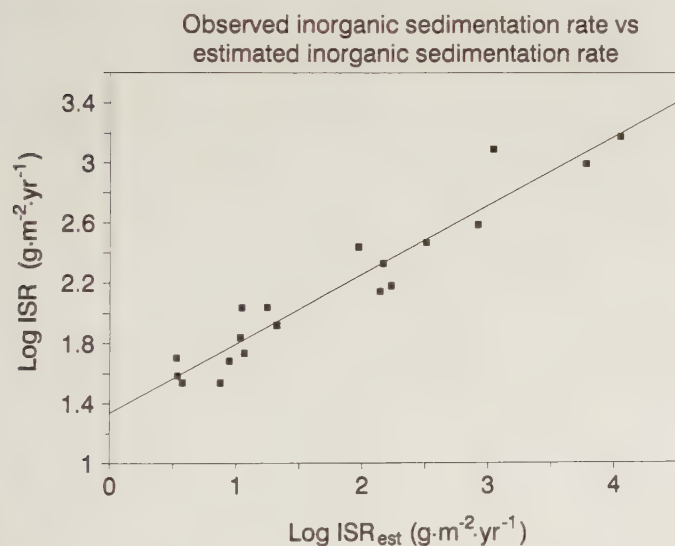


FIG. 1. Plot of observed inorganic sedimentation rate (ISR) versus estimated inorganic sedimentation rate (ISR_{est}) (eq. 1). The line represents the best fit linear regression (eq. 3).

ISR_{est} of comparable magnitude, suggesting that deltaic sedimentation is balanced by autochthonous inorganic sedimentation. The relationship (eq. 3) provides a more direct measure of inorganic sedimentation rates than either inorganic sediment loads (eq. 2) or ISR_{est} (eq. 1), since it appears to adjust ISR_{est} for the effects of autochthonous and deltaic inorganic sedimentation. A mass-balance approach to predicting sedimentation rates from ISR_{est} that includes dissolved silica, calcium carbonate, organic matter, and nutrient

inputs, as well as deltaic sedimentation, would be preferable, but the data base to construct such a model does not exist.

Profundal Sediment Organic Content and Physical Character versus Inorganic Sedimentation Rate (ISR_{pred})

The sediment organic content ranges from 3 to 62% of dry weight at maximum depth in 83 lakes. Lakes with a high sediment organic content (30–62% of the dry weight) normally have low ISR_{pred} of 20–150 g·m⁻²·yr⁻¹ and occur in catchments of igneous and high-grade metamorphic rocks such as the shield regions of southern, central, and western Ontario, Quebec, New Hampshire, and northeastern Minnesota (Tables 1 and 2). Lakes with catchments of sedimentary and low-grade metasedimentary rocks, such as those in the Eastern Townships of Quebec, Lake Memphremagog, lakes in northern Illinois, and Sunfish Lake, have intermediate ISR_{pred}, usually between 150 and 400 g·m⁻²·yr⁻¹, and are characterized by intermediate sediment organic contents (10–30% of dry weight) (Tables 1 and 2). Within each of these two broad classifications, larger and/or lakes with higher ISR_{pred} tend to have lower organic contents. The Laurentian Great Lakes have a low organic content (6–15%) regardless of ISR_{pred}, suggesting for these lakes that extreme exposures and the resulting currents determine organic content. Lastly, large lakes, such as Great Slave, Constance, and Geneva with their very high ISR_{pred} (over 1000 g·m⁻²·yr⁻¹), have the lowest organic contents, 3, 6, and 7%, respectively (Table 2).

Sediment water content and bulk density show a similar pattern in 71 and 52 lakes, respectively. Sediment water contents generally range between 92 and 99% for shield lakes, between 83 and 92% for lakes with sedimentary catchments, and between 71 and 83% for Constance, Geneva, and the Laurentian Great Lakes. Sediment bulk density of shield lakes is gen-

erally between 1.020 and 1.050 g·mL⁻¹, between 1.050 and 1.100 g·mL⁻¹ for lakes with catchments of sedimentary rocks, and between 1.100 and 1.209 g·mL⁻¹ in the Laurentian Great Lakes and other large lakes.

Correlation Matrix

Organic content and water content are highly positively correlated, and both are highly negatively correlated with bulk density (Table 3). Both organic content and water content are negatively correlated with ISR_{pred} , predicted net organic sedimentation rate (OSR_{pred}), lake surface area, exposure, and maximum depth. Bulk density is positively correlated with ISR_{pred} , OSR_{pred} , lake surface area, exposure, and maximum depth (Table 3). The negative correlation of OSR_{pred} with sediment organic content suggests that the input of organic matter to lake sediments has less influence on the sediment organic content than does the rate of inorganic sedimentation. Thus, OSR_{pred} is not considered in multiple regressions.

Lake surface area and exposure are extremely highly inter-correlated (+, $R = 0.99$) and both are weakly correlated (+) with ISR_{pred} and OSR_{pred} , which are also highly intercorrelated (+) (Table 3). Maximum depth is positively correlated with lake surface area, exposure, and ISR_{pred} . Chlorophyll *a* is not significantly correlated with any of the sediment or morphometric parameters.

Multiple Regressions Predicting Profundal Sediment Organic Content and Physical Character

To test the hypothesis that the rate of inorganic sedimentation is the main determinant of sediment organic content and physical character, multiple regressions were carried out relating the dependent variables organic content, water content, and bulk density against ISR_{pred} and the other predictors, exposure, lake surface area, maximum depth, and a categorical variable for core depth (0 for 0–5 cm core depth, 1 for 0–10 or 20 cm). Only ISR_{pred} and exposure (or lake area) are significant predictors. The multiple regression predicting sediment organic content from ISR_{pred} and lake surface area explains 76% of the variation in organic content (Fig. 2) (eq. 4, Table 4). The multiple regression with ISR_{pred} and exposure (eq. 5, Table 4) explains 77% of the variation in organic content and is not significantly different from eq. 4 in intercept or coefficients. In fact, the coefficients for the energy terms (exposure and lake surface area) are identical, which is not surprising given the high intercorrelation of the two terms. In these regressions (eq. 4 and 5, Table 4), ISR_{pred} and the energy term make similar contributions to the explained variation. The intercepts of these regressions are not significantly different from 100%

organic content. Thus, as the ISR_{pred} and exposure (or lake area) decrease, organic content approaches 100% (eq. 4 and 5, Table 4).

Regressions predicting water content from ISR_{pred} and either lake surface area or exposure explain 74 and 77% of the variation in sediment water content, respectively (eq. 6 and 7, Table 4). Again, these regressions are not significantly different from each other in intercept or coefficients. The energy term (lake surface area or exposure) explains nearly twice as much of the variation in water content as does ISR_{pred} and suggests that the energy of the depositional environment is more important than inorganic sedimentation as a determinant of sediment water content. The intercepts for water content are not significantly different from 100% water content, indicating that as ISR_{pred} and exposure (or lake area) decrease, water content approaches 100% (eq. 6 and 7, Table 4).

Bulk density can also be predicted by ISR_{pred} and either lake surface area or exposure (eq. 8 and 9, Table 4). The regression containing ISR_{pred} and lake surface area explains 66% of the variation in bulk density (eq. 8, Table 4), while that containing ISR_{pred} and exposure explains 64% of the variation in bulk density (eq. 9, Table 4). Once again, differences in coefficients and intercepts are not statistically significant. ISR_{pred} contributes slightly more to these regressions than the energy factors (lake surface area or exposure). Once again, as ISR_{pred} and exposure (or lake area) decrease, bulk density approaches 1.0 g·mL⁻¹ (eq. 8 and 9, Table 4).

Discussion

These findings support the hypothesis that an increase in the inorganic sedimentation rate and exposure (lake surface area) results in lower organic content and water content, and greater bulk density of profundal sediment. The fact that the intercepts of these regressions converge at either 100% water content or organic content as ISRs and exposure (or lake area) decrease provides additional support for the statistical result. Due to the great range in lake surface area and exposure (over 6 orders of magnitude), the two terms appear interchangeable. However, when morphometry is complex, the departure between lake surface area and exposure can be large, and in those situations, we recommend exposure as the better surrogate for the energy of the depositional environment. The correlations between maximum depth and profundal sediment organic content and physical character are probably the result of the correlation between maximum depth and lake area (Table 3) because when the maximum depth is considered in multiple regressions with lake area, it is not statistically significant. The categorical variable representing potential bias due to different coring depths

TABLE 3. Correlation matrix of organic content (OC), water content (WC), bulk density (BD), maximum depth (h_{max}), chlorophyll *a* (CHLA), lake surface area (SA), predicted inorganic sedimentation rate (ISR_{pred}), and predicted organic sedimentation rate (OSR_{pred}). All terms are logarithmically transformed except for WC. * $P < 0.05$; ** $P < 0.01$; all others, $P < 0.0001$.

	OC	WC	BD	h_{max}	CHLA	SA	ISR_{pred}	OSR_{pred}
OC	—	0.87	-0.86	-0.59	—	-0.75	-0.73	-0.60
WC		—	-0.88	-0.61	—	-0.81	-0.65	-0.53
BD			—	0.49	—	0.68	0.73	0.67
h_{max}				—	—	0.81	0.27*	—
CHLA					—	—	—	—
SA						—	0.45	0.35**
ISR_{pred}							—	0.98
OSR_{pred}								—

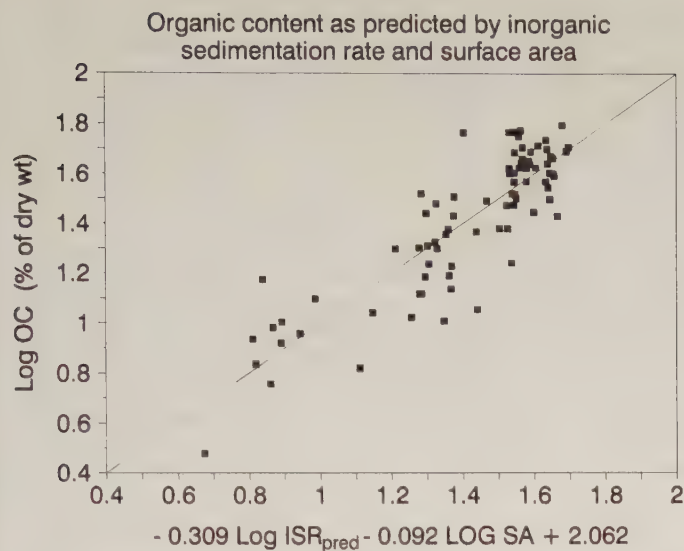


FIG. 2. Sediment organic content (OC) of sediment from maximum depth in 83 lakes versus that predicted from a multiple regression of predicted inorganic sedimentation rate (ISR_{pred}) and lake surface area (SA) (eq. 4). The line represents the 1:1 correspondence between observed and predicted organic content.

is not statistically significant, indicating that the literature data are compatible with those collected for this study.

Between-lake variation in sediments not explained by ISR_{pred} and lake surface area should be attributable either to differences in the quartz, clay, calcium carbonate, or iron content of the inorganic matter or to extremely high or low sedimentation of autochthonous or allochthonous organic matter.

Predicting Sedimentation Rates from Sediment Loads

We have demonstrated how estimates of inorganic sedimentation rates (eq. 1), obtained from catchment inorganic sediment loads (eq. 2) and corrected for sediment retention and

sediment focusing, can be used to accurately predict inorganic sedimentation rates (eq. 3). Although this model is mechanistically simplistic, its predictions are essential for testing the hypothesis that inorganic sedimentation influences profundal sediment organic content and physical character because sedimentation rates are available for only 19 of the 83 lakes in our data set. Measured sedimentation rates are not commonly available for most lakes, and more than 50% of the sedimentation rates we obtained from the literature are from some of the best-studied lakes in the world, including the Laurentian Great Lakes, Mirror Lake, Lake Constance, and Lake Geneva. We are presently refining the model (eq. 3) through a mass-balance approach by including inputs of dissolved silica, calcium carbonate, organic matter, and nutrients, along with a deltaic sedimentation term.

Predicting Sediment Organic Content and Physical Character from Inorganic Sedimentation Rates

Predicted inorganic sedimentation rate and lake area explain much of the between-lake variation in organic content (eq. 4 and 5, Table 4), water content (eq. 6 and 7, Table 4), and bulk density (eq. 8 and 9, Table 4). These results confirm the hypothesis that inorganic sedimentation and the energy of the depositional environment determine the organic content and physical character of profundal sediments. Regression models predicting sediment organic content and bulk density exhibit similar contributions from inorganic sedimentation and from surrogates for the energy of the depositional environment. In multiple regression models predicting water content, however, the energy of the depositional environment appears to play a greater role. This is reasonable because the entrainment of cohesive sediments is largely a function of water content, and sediments with lower water content are more stable under higher energy conditions than those with higher water contents. Thus, in the Laurentian Great Lakes and other large lakes in our data set, the effects of currents on sediment water content appear to predominate.

TABLE 4. Significant multiple regressions of predicted inorganic sedimentation rate (ISR_{pred}) and either exposure (E) or lake surface area (SA) as predictors of organic content (OC), water content (WC), and bulk density (BD).

	Eq. 4 log OC	Eq. 5 log OC	Eq. 6 WC	Eq. 7 WC	Eq. 8 log BD	Eq. 9 log BD
Constant	2.062 (0.078)	2.084 (0.090)	101.599 (1.993)	102.657 (2.227)	-0.011 (0.007)	-0.012 (0.008)
log ISR_{pred}	-0.309 (0.039)	-0.319 (0.043)	-4.858 (1.016)	-5.326 (1.109)	0.019 (0.003)	0.020 (0.004)
log E		-0.092 (0.011)		-2.314 (0.257)		0.004 (0.001)
log SA	-0.092 (0.011)		-2.275 (0.249)		0.004 (0.001)	
R^2	0.755	0.766	0.740	0.767	0.662	0.644
SE_{est}	0.144	0.146	3.069	3.085	0.010	0.011
n	83	71	71	63	52	44

Lake trophic status, represented by chlorophyll *a*, is not significantly related to sediment organic content, water content, or bulk density. Inorganic sedimentation rates are much more variable across lakes than organic sedimentation rates, and thus it is reasonable that sediment organic content and physical character are primarily determined by the input of inorganic matter to the basin rather than by trophic factors. Indeed, some of the highest organic content sediment (and lowest ISR_{pred}) are found in the Laurentian Shield lakes, which are the most oligotrophic lakes that we studied. This potentially counterintuitive observation has been noted previously (Brunskill et al. 1971) but never explained.

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Comparison of Otolith-Based Back-Calculation Methods to Determine Individual Growth Histories of Larval Striped Bass, *Morone saxatilis*¹

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In rearing studies on 6- to 22-d-old larval striped bass, *Morone saxatilis*, we applied several back-calculation methods to known-growth larvae. A growth effect occurred on otolith diameter – standard length relationships, where slower growing larvae had relatively larger otoliths. Otolith growth was less affected by feeding regime than was somatic growth. Due to the conservative nature of otolith growth, proportional based (Biological Intercept Method) and simple linear regression methods linearized somatic growth transitions and did not estimate periods of negative growth. A quadratic regression method which used age as an additional predictor resulted in the accurate back-calculation of size at age in all groups of laboratory-reared larvae. However, when model coefficients were applied to a test population of pond-reared larvae, the quadratic model performed poorly. While differences in relative otolith size between pond- and laboratory-reared larvae could be ascribed to a temperature effect, the inability to apply the model also indicates a problem specific to regression-based methods. Theoretical rationale and experimental proof provided evidence for the inclusion of age in back-calculation models, but parameterization will have to occur for each field application.

Nous avons appliqué plusieurs méthodes de calcul à rebours au cours d'études de la croissance de larves de bar rayé âgées de 6 à 22 jours. Un effet de la croissance a été noté sur le rapport entre le diamètre de l'otolithe et la longueur standard, les larves à croissance plus lente présentant des otolithes relativement plus gros. La croissance des otolithes était moins affectée par le régime alimentaire que la croissance somatique. Étant donné la nature assez constante de la croissance des otolithes, les méthodes proportionnelles (droite au point d'interception) et les méthodes par régression linéaire simple ont tendance à rendre linéaires les transitions de croissance somatique et à ne pas estimer les périodes de croissance négative. La méthode de régression quadratique qui fait appel à l'âge comme paramètre de prévision supplémentaire a permis de calculer de façon exacte la taille antérieure selon l'âge de tous les groupes de larves élevées en laboratoire. Mais l'application des coefficients du modèle à une population expérimentale en étang n'a pas permis d'obtenir de bons résultats. Les écarts entre la taille relative des otolithes des larves élevées en étang ou en laboratoire pouvait être attribués à la température, mais l'impossibilité d'appliquer le modèle s'expliquait aussi par des problèmes liés aux méthodes basées sur les régressions. La théorie et les résultats expérimentaux appuient l'utilisation de l'âge dans les modèles de calcul à rebours, mais les paramètres devront être établis pour chaque application sur le terrain.

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Field testing of size-selective mortality has required back-calculation of individual growth rates obtained from otolith microstructure (Rosenberg and Haugen 1982; Crecco and Savoy 1985; Neilson and Geen 1985; Penney and Evans 1985; Post and Prankevicius 1987). Two decades ago, Pannella (1971) observed "microincrements" within the microstructure of otoliths and conjectured that (1) increments were formed daily and (2) individual increment widths were a record of daily somatic growth. Pannella's (1971) first hypothesis has been verified for dozens of species (Campana and Neilson 1985; Jones 1986; Secor et al. 1991), and the term "daily incre-

ments" has replaced microincrements under the inference that daily increment formation is general to teleosts. On the other hand, many exceptions have occurred for the second hypothesis (Bradford and Geen 1987; Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; Secor et al. 1989; Wright et al. 1990). Despite 20 yr of concerted effort, investigators have not been able to quantify a comprehensive or accurate relation between otolith growth rate and somatic growth rate.

Confirmation of daily increment formation has relied on known-age (or known-interval) samples (Jones 1986; Geffen 1987). Thus, to correctly decode increment widths into somatic growth information, the growth history of the fish must be known as well. Further, the accuracy of the back-calculation method should be tested on fish reared in conditions which approach those of the natural environment (Rosenberg and Haugen 1982; Secor et al. 1989). The true success of any general back-calculation model will be through its application and adjustment to varied growth situations.

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TABLE 1. Experimental feeding regimes.

Treatment	Description	Days after hatch when <i>Artemia</i> first supplied	Ration (<i>Artemia</i> /mL)
Feed-1	Delayed 10 d	16	1
Feed-2	Delayed 4 d	10	1
Feed-3	Fed low food concentration	6	0.5
Feed-4	Fed medium food concentration	6	1
Feed-5	Fed high food concentration	6	3

In this report we examine the relationship between otolith and somatic growth and contrast back-calculation methods for laboratory-reared larval striped bass, *Morone saxatilis*, with widely varying known growth rates. Three hypotheses about otolith growth were tested: (1) growth (age and feeding regime) affects relative otolith size (the relationship between otolith and fish size), (2) daily otolith growth is positive during negative somatic growth and is less variable than somatic growth rate in response to feeding regime, and (3) residual patterns in the otolith – fish size regression provide information about individual growth rates. Observed size at age for larvae with various growth histories was compared with back-calculated size at age using four methods: the Simple Regression Method, the Biological Intercept Method, the Multiple Regression Method, and the Quadratic Response Method. Laboratory-parameterized back-calculation methods were tested on pond-reared larvae experiencing more natural growth conditions.

Back-Calculation Methods

The most common method to interpret increment widths (Simple Regression Method) is to regress fish size on otolith size and estimate fish size at age (F_t) through the following formula:

$$F_t = b \cdot O_t + a$$

where O_t is otolith size corresponding to age t , and b and a are the regression slope and intercept, respectively. However, recent studies have shown a “growth effect” where slower growing fish have disproportionately larger otoliths (Marshall and Parker 1982; Reznick et al. 1989; Secor and Dean 1989; Secor et al. 1989). Temperature (Mosegaard et al. 1988; Tzeng and Yu 1989), location (Taubert and Coble 1977), and season (Tzeng and Yu 1988) can also influence the manner in which fish size scales to otolith size. Finally, the Simple Regression Method is indirect and insensitive to changes in individual growth histories due to its averaging effect (Secor et al. 1989). The objective of determining individual growth rates is compromised, since growth differences among individuals, manifested as residuals in the otolith – fish length-regression, are ignored.

Alternatives to the Simple Regression Method include the use of additional predictors available from field studies (Multiple Regression and Quadratic Response Methods) and a recently proposed modified Lee's Method (Biological Intercept Method) (Campana 1990). Multiple and quadratic regressions using temperature and age effects can explain a significant portion of the variance in the residuals of the simple otolith – fish size regressions (Mosegaard et al. 1988; Secor et al. 1989). The Biological Intercept Model was recently suggested by Campana (1990) as a method to circumvent the growth effect. Campana (1990) modified the Fraser–Lee formula as follows:

$$F_t = F_c + (O_t - O_c) \cdot (F_c - F_o) \cdot (O_c - O_o)^{-1}$$

where F_t and F_c are standard length (SL) at age and at capture, respectively, O_t and O_c are otolith diameter at age and at capture, respectively, and F_o and O_o are SL and otolith diameter corresponding to “the initiation of proportionality between fish and otolith growth” (Campana 1990). He predicted that the model is robust to the growth effect because it levers from a more realistic intercept value.

Methods

Known-Growth Experiments

We varied maternal and feeding regime factors to provide larval striped bass with various known growth histories. Experimental treatments were run simultaneously to control for any variance in temperature or rearing practices. Four broods (B1, B2, B3, and B4) of maternal half-sibs were provided by the Jack D. Bayless Fisheries Research Hatchery (St. Stephens, South Carolina). All broods were hatched within 8 h of each other. Rearing techniques, feeding treatments, and water quality are described in Secor (1990). Briefly, 3-d-old prolarvae (terminology after Balon 1981) were stocked into 15-L tanks at densities of 16.7 larvae/L. Mean daily minimum and maximum temperatures were 18.9 ± 1.4 (sd) and $20.0 \pm 1.0^\circ\text{C}$, respectively. Forty tanks comprised five feeding regimes (Table 1) and four experimental broods, with each feeding regime-brood combination replicated twice. Larvae were sampled ($N = 4-6$) on days 7, 10, 13, 16, 19, and 22 and preserved in 95% ethanol. Mortality was observed daily and rates only significantly varied between Feed-1 and the rest of the feeding treatments (Secor 1990). Survival of Feed-1 treatment averaged 31%; survival of the other treatments averaged 81%. Six-day-old larvae were also stocked into pens within earthen grow-out ponds as described in Secor (1990). Pens had volumes of 0.5 m^3 and were stocked with 500 larvae from each experimental brood. Samples were taken at 7, 10, 13, 16, and 20 d. Daily minimum and maximum temperatures averaged 23 ± 1.9 and $26.1 \pm 3.2^\circ\text{C}$, respectively. Notochord lengths or SL were measured according to Rogers and Westin (1981) under $60\times$ magnification by projecting the image on a digitizing pad and tracing the notochord or vertebral column. Larval shrinkage rate was dependent on size and varied between 4.1% for 5-mm larvae and 1.2% for 11-mm larvae (Secor 1990). Since ultimate field application of back-calculation methods will be made on ethanol-preserved material, larval lengths were not corrected for shrinkage. Sagittae were dissected and measured as described below.

Otolith Growth Measures

Investigators have measured otoliths by single-dimension growth axes. Common measures have included maximum otolith diameter (Radtko and Dean 1982; Rice et al. 1985; Reznick et al. 1989; Secor and Dean 1989), maximum otolith radius

(Savoy and Crecco 1987; Tzeng and Yu 1989), a prescribed axis (radius) which occurs in a similar area among otolith sections (Wilson and Larkin 1982; Bradford and Geen 1987; Eckmann and Rey 1987; Mosegaard et al. 1988), or any axis which has the most easily resolved increments (Campana 1984; Volk et al. 1984). We measured otolith growth by digitized otolith areas. The method avoided subjective decision making about which axis is measured and also provided more information, since it is two-dimensional (Michaud et al. 1988).

Whole right sagittae were projected under $300\times$ magnification onto a digitizing pad with a camera lucida and their perimeters were traced in lateral perspective. From the digitized perimeter (P), imaging software calculated a maximum length and otolith diameter ($P \cdot \pi^{-1}$). Otolith diameter thus represented an unbiased measure of otolith size based on two dimensions, and maximum otolith diameter represented an objective measure of the single largest axis through the otolith. Precision error in replicate measures of otolith diameter and maximum diameter was 1.3 and 2.3%, respectively (Secor 1990).

Because back-calculation methods required that otoliths be embedded and polished, several experimental treatments and replicates were omitted from further analysis to reduce labor. For the tank experiments, two experimental broods (B2 and B4) and four feeding regimes (Feed-1, Feed-2, Feed-3, and Feed-5) were selected, since they represented sufficient intermediate and extreme growth values over all experimental treatments. Five otoliths were prepared for back-calculation from single replicates for each brood-feeding regime combination (total = 40 otoliths). In the pen experiment, back-calculation models were applied to two broods (B1 and B4). Ten samples were analyzed from each of these broods (total = 20 otoliths).

Right sagittae sampled at the end of the experiments (22 d for tank experiments and 20 d for pen experiments) were prepared for back-calculation methods according to Secor et al. (1991). To permit application of otolith growth models derived from whole otoliths, thin sections of otoliths were prepared in the sagittal plane (in lateral perspective). Otoliths obtained from the Feed-1 treatment contained increments which were not resolvable with light microscopy and had to be prepared for scanning electron microscopy (SEM) analysis. These larvae were embedded whole (Haake et al. 1982) and their sagittae polished and decalcified with 7% EDTA (pH = 7.5) for 1–3 min. Most sagittae from Feed-1 fish were sectioned at angles oblique to the sagittal plane (Fig. 1), and otolith diameter, a measure specific to the sagittal plane, could not be directly measured. These otoliths were sectioned consistently through the longest axis of the otolith so maximum length could be measured. Maximum length was then translated into otolith diameter with a regression calculated for this treatment from whole otoliths (otolith diameter (micrometres) = $-5.524 + 1.104 \cdot \text{maximum length (micrometres)}$; $N = 152$, $R^2 = 0.78$). All increments in these sections could be identified.

To digitize areas corresponding to otolith diameter at age (O_t), the increments corresponding to the sampling days were first identified. Secor and Dean (1989) found that first increment formation for Santee-Cooper striped bass occurred at 4 d after hatch and subsequent increments were formed daily. Therefore, the fourth discontinuous zone (sensu Tanaka et al. 1981) corresponds to the seventh day after hatch. Likewise, collection days 10, 13, 16, and 19 corresponded to increment numbers 7, 10, 13, and 16. To insure that these increments were accurately traced, a camera lucida projected the otolith's image onto paper and increments corresponding to sample dates were traced (Fig. 1 and 2). A stage micrometer projection was also traced



A



B

FIG. 1. Digitized otolith microstructure of Feed-1 larva. Otolith microstructure was digitized by drawing increments corresponding to days 7, 10, 13, 16, 19, and 22. (A) Scanning electron micrograph of Feed-1 (see Table 1) larval otolith (SL = 5.3 mm); (B) same otolith viewed under higher magnification. Every third discontinuous zone is labelled with a large arrowhead and number. Other discontinuous zones are labelled with small arrowheads.

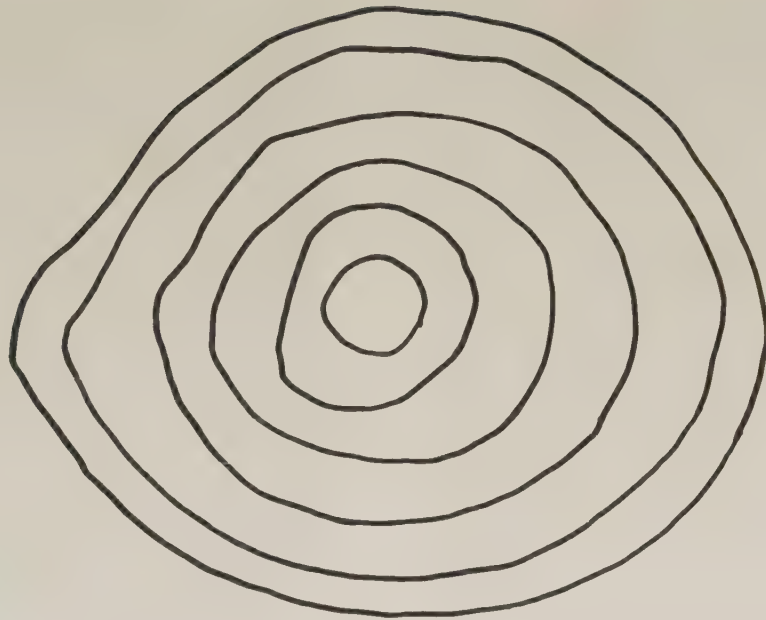


FIG. 2. Light micrograph of Feed-5 (see Table 1) larval otolith (SL = 10.2 mm). Every third discontinuous zone was traced with the aid of a camera lucida (see text for details). Bar = 100 μ m.

so that the increment "drawings" were properly scaled. Each traced discontinuous zone was digitized and maximum length and otolith diameters calculated. Similarly, for the Feed-1 treatment larvae, increments corresponding to sampling days were digitized from SEM micrographs. Precision error in drawing and digitizing increments was 4.5% for otolith diameter (Secor

1990). To confirm that increments were correctly identified and drawn, average digitized areas for each age were compared with whole-otolith dimensions at the same ages across brood and feeding treatment levels. Digitized increments corresponded well to whole-otolith measures (Fig. 3). This analysis also indicated that mortality during the experiments was not size selective.

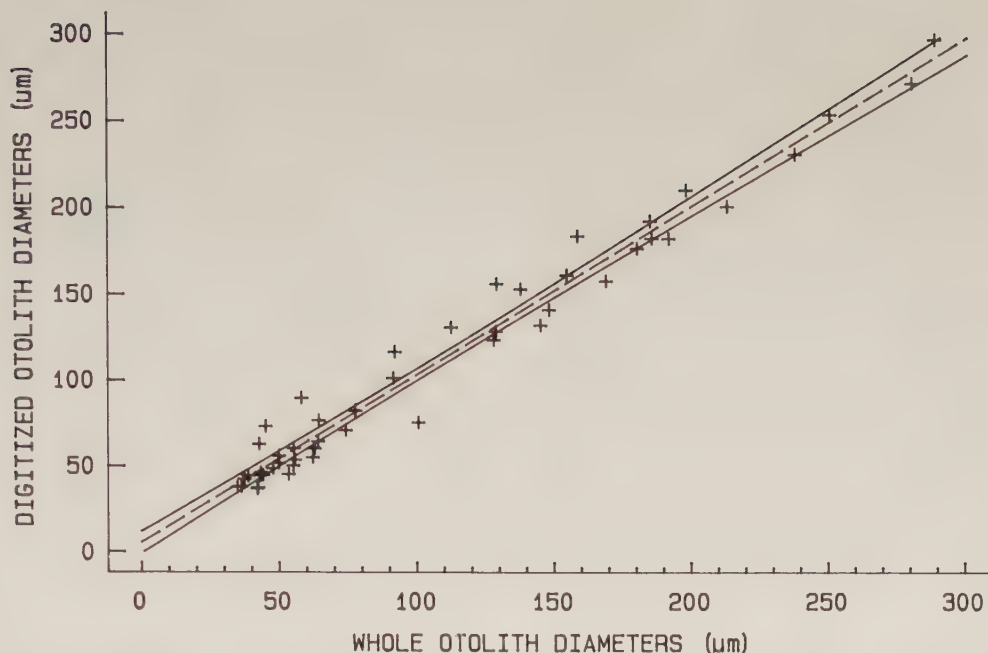


FIG. 3. Comparison of otolith dimensions from drawn increments and whole-otolith measures taken from samples collected at intermediate ages. Average diameters from digitized and whole otoliths were paired for each brood·feed·age level. Digitized otolith diameter = $5.338 + 0.983 \cdot \text{whole otolith diameter}$; $N = 48$, $F = 1634$, $R^2 = 0.97$.

Analysis

Analysis of back-calculation models used only otolith diameter, since it was more precise than maximum length (Secor 1990). Otolith diameter and maximum length were highly correlated ($R^2 = 0.99$, $N = 953$, $F = 160,073$; otolith diameter (micrometres) = $-4.54 + 0.89 \cdot \text{maximum length}$), so results given for otolith diameter are directly applicable for otolith maximum length as well. The coordinates F_o and O_o , for the Biological Intercept Method needed to be empirically determined. Unfortunately, there is no clear point where larval (or embryo) size and otolith size become "proportional". Campana (1990) suggested that otolith and fish size at hatching be used if subsequent fish – otolith growth is proportional. However, considerable variation exists in fish size at hatching. Alternatively, we reasoned that the point of initial increment formation would be a conservative estimate of the incipience of proportionality. Therefore, the biological intercept was determined as the mean otolith diameter and larval length at 5 d after hatch. Because back-calculation methods were compared on a brood-specific basis, a biological intercept was calculated for each brood (B1: $O_o = 30.2$, $F_o = 5.00$; B2: $O_o = 28.2$, $F_o = 4.87$; B3: $O_o = 31.0$, $F_o = 5.21$; B4: $O_o = 32.2$, $F_o = 5.21$).

Otolith growth models using the Simple Regression Method, the Multiple Regression Method, and the Quadratic Response Method were developed by regressing SL on otolith diameter, age, and otolith diameter·age predictors for all treatment samples taken throughout the rearing studies. A Forward Stepwise Regression procedure (SAS) was used to determine which predictors significantly improved the overall model. Predictors were added singly, and after each addition the procedure removed variables which did not significantly improve the overall model or failed to significantly contribute after the addition of another variable. Linear, cross-product, and quadratic effects in the quadratic response procedure were contrasted with

sequential sums of squares (SAS: PROC RSREG). The regression-based methods and the Biological Intercept Method were applied to the digitized otolith drawings representing samples collected at the end of the experiments. Averages and 95% confidence intervals were calculated through Multiple Analysis of Variance (STATGRAF) across feeding treatments for each age·brood combination. These statistics were then compared with fish lengths measured from larvae collected on intermediate sample dates (observed growth rates).

Results

Growth Effect

Feeding regime had less effect on otolith diameter (27% of variance) than on SL (35% of variance) (Table 2). However, age showed greater effects on otolith diameter (60% of variance) than SL (53% of variance) (Table 2). To further inspect differences between otolith growth and somatic growth, plots of otolith and larval sizes at age were overlayed across the experimental broods for four feeding regimes (Fig. 4). In starvation–feeding regimes where larvae experienced negative somatic growth, otoliths grew at a fairly linear rate. During long-term starvation, otolith growth remained positive but declined with age, especially for broods B1 and B2. After food was initially supplied, fish length increased at a higher rate than did otolith diameter. In larvae fed throughout the study, larval length displayed growth inflections, but otolith growth was generally linear and reflected these inflections in a less marked manner.

SL and otolith diameter were linearly correlated with a high coefficient of determination ($R^2 = 0.92$) (Fig. 5A). Residuals showed no consistent relationship with otolith diameter. Using otolith diameter as a covariate, significant feeding ration effects were observed on SL ($F = 68.72$, $P < 0.0001$, $N = 954$). Feeding regimes showing lower growth rates (Fig. 4; Table 3)

TABLE 2. Analysis of variance on the effect of feeding regime (feeds) and age on either otolith diameter ($N = 955$) or SL ($N = 964$). SS = sum of squares. *Effect significant ($P < 0.001$).

Factor	Among feeds			Within feeds		Among ages			Within ages	
	SS	df	F	SS	df	SS	df	F	SS	df
Otolith diameter	1473119	4	89.1*	3925160	950	3279058	5	293.7*	2119221	949
SL	1214.14	4	130.7*	2226.9	959	1828.8	5	217.3*	1612.2	95

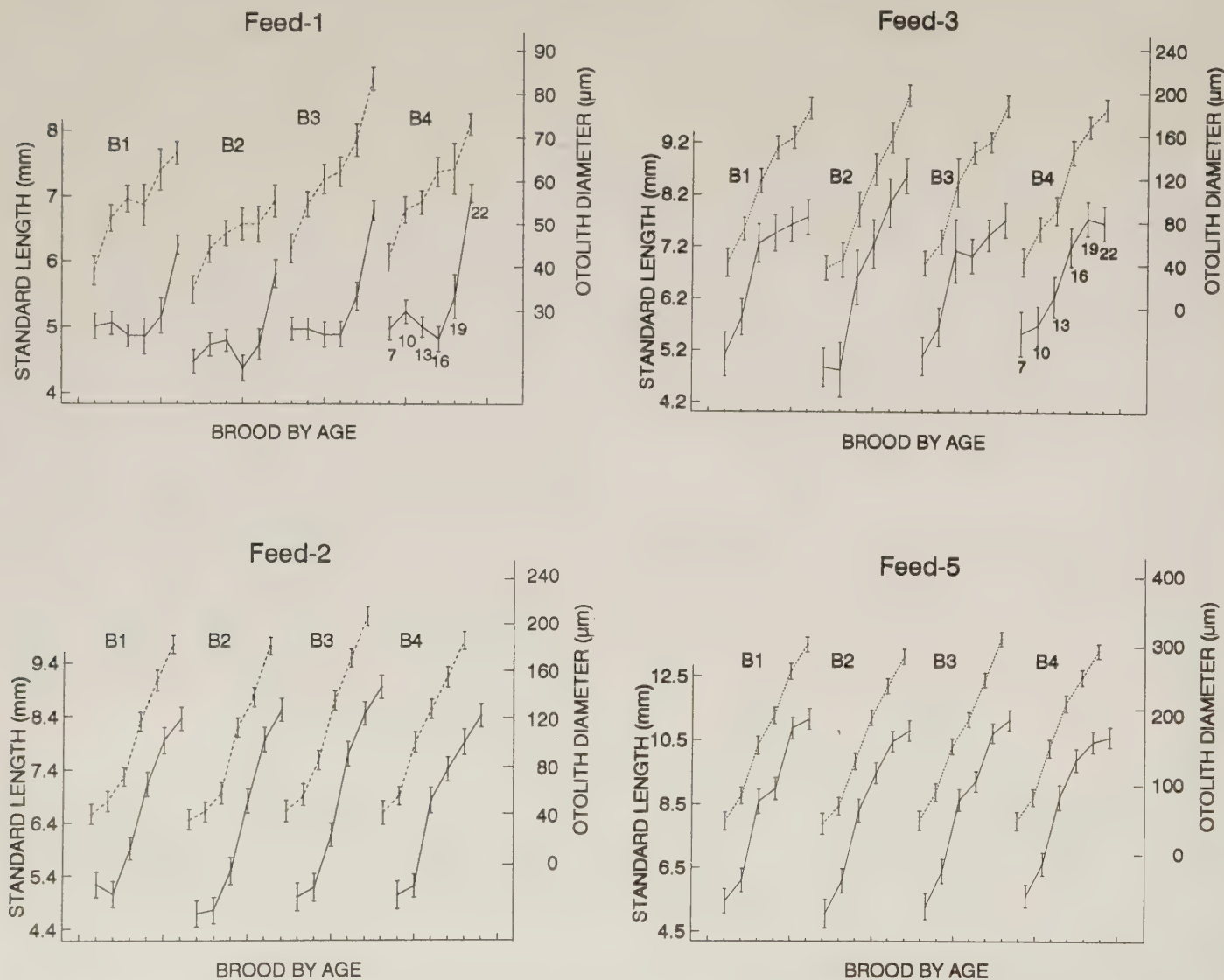


FIG. 4. Comparison of 95% confidence intervals for otolith diameter and standard length by feeding treatment and age. Each panel contains four somatic and otolith growth curves, one for each brood. SL (solid lines) are scaled on the left axis. Otolith diameters (broken lines) are scaled on the right axis. Ages are listed below confidence limit bars only for brood B4 of the top panels. All broods follow this designation. Feed-4 showed similar somatic and otolith growth patterns to Feed-5 and was not included in this demonstration. See Table 1 for feeding regime abbreviations; see Table 3 for somatic growth rates.

contained larvae with relatively larger otoliths (Fig. 5B and 5C). The overall trend was a systematic decrease in relative otolith size with increasing feeding ration. For Feed-1 larvae, the intercept has shifted downward due to the skewed distribution of negatively growing larvae. The lower intercept has caused the slope to inflect positively. However, part of the slope was also explained by age effects where small larvae are very old for their size and therefore have disproportionately large otoliths. By visually overlaying Fig. 5A, 5B, and 5C, one observes that within the distribution of the paired data points

(Fig. 5A), a myriad of growth-dependent scaling relations can occur (Secor and Dean 1989; Campana 1990).

Regression-Based Back-Calculation Methods

SL of all tank-reared larvae were regressed on otolith diameter and age variables (Table 4). The predictors otolith diameter, age, their cross-product, and quadratic terms were accepted in a hierarchical stepwise procedure due to the improvement of fit to the overall model (Table 5). Terms in the Quadratic Response Method were included on the basis of

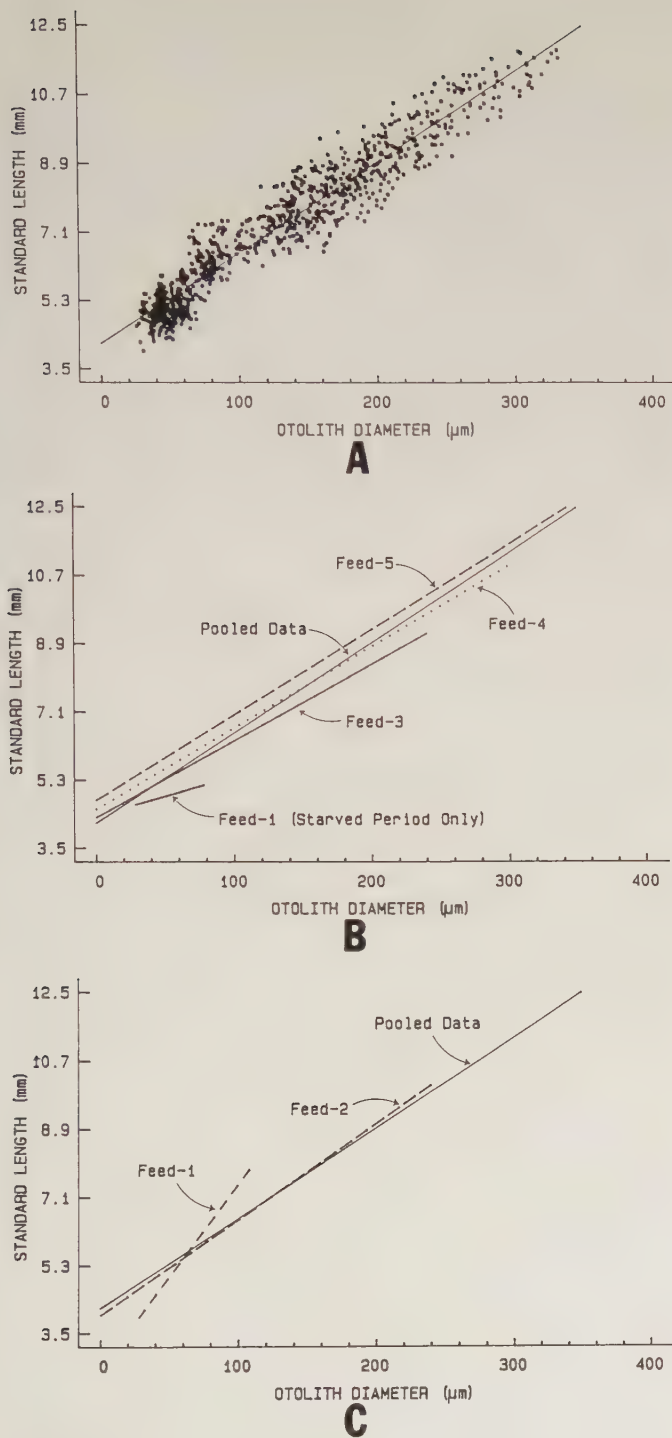


FIG. 5. Relations between SL and otolith diameter for tank-reared larvae. (A) Overall regression for combined feeding regimes: $SL = 4.160 + 0.0239 \cdot \text{otolith diameter}$; $N = 955$, $R^2 = 0.917$. (B) Regression lines for Feed-1, Feed-3, Feed-4, Feed-5, and the overall regression. Regression for Feed-1 included data only for the starvation period (age = 7, 10, 13, and 16 d). Feed-1 (starved): $SL = 4.354 + 0.0105 \cdot \text{otolith diameter}$; $N = 105$, $R^2 = 0.095$. Feed-3: $SL = 4.313 + 0.0203 \cdot \text{otolith diameter}$; $N = 186$, $R^2 = 0.892$. Feed-4: $SL = 4.529 + 0.0215 \cdot \text{otolith diameter}$; $N = 206$, $R^2 = 0.937$. Feed-5: $SL = 4.767 + 0.0226 \cdot \text{otolith diameter}$; $N = 201$, $R^2 = 0.947$. (C) Regression lines for Feed-1, Feed-2, and the overall regression. Regression for Feed-1 includes data before and after food was first supplied. Feed-1: $SL = 2.537 + 0.0491 \cdot \text{otolith diameter}$; $N = 155$, $R^2 = 0.609$. Feed-2: $SL = 3.973 + 0.0254 \cdot \text{otolith diameter}$; $N = 207$, $R^2 = 0.946$. See Table 1 for feeding regime abbreviations.

a contrast of the types of effects: linear ($F = 9052$, $P < 0.001$), cross-product ($F = 607$, $P < 0.001$), or quadratic ($F = 354$, $P < 0.001$). The coefficient of determination and fit of the model significantly improved from the simple linear to the quadratic effects which verified the use of all terms in this model.

Age and otolith length were collinear in the multiple and quadratic regression models (Table 2; Fig. 4). To verify that age acted independently of otolith length in the models, an analysis of residuals of the otolith – fish size regression (Fig. 5A) was performed. Residuals were significantly related to age for each feeding regime (Table 6). Patterns in residuals reflected changes in size at age (Fig. 6). Observed growth inflections were amplified in the residuals. Periods of declining positive growth rate and growth stasis corresponded to negative residuals, and positive changes in somatic growth rate resulted in positive residuals. This analysis indicated that when somatic growth rate declined, an accumulation of days (i.e. increase in age and otolith size) relative to fish length caused residuals to become negative.

Application of Methods

Back-calculation methods were applied to broods B2 and B4 because they showed considerable somatic growth differences across feeding levels (Fig. 4 and 7). Negative growth was observed for Feed-1 over a 9-d period for both broods. A period of accelerated growth was observed in Feed-2, Feed-3, and Feed-5 between 13 and 16 d. Beyond 16 d, growth rates tended to decline in these treatments. Overall, the Feed-1 growth curves were exponential whereas the others were typified by a sigmoid curve.

In back-calculation applications, the Biological Intercept Method behaved quite similarly to the Simple Regression Method (Fig. 7). Neither method showed negative growth for Feed-1, and the positive bias was greater for the Biological Intercept for this treatment level. The methods both tended to linearize growth patterns. This was expected given the conservative nature of otolith growth (Table 2; Fig. 4). Confidence intervals were greater for the Biological Intercept Method because it incorporated the variance of fish and otolith size at capture.

Back-calculated growth curves using the Multiple Regression Method and Quadratic Response Method matched observed growth patterns much closer than the other methods (Fig. 7). In Feed-2, Feed-3, and Feed-5 levels, the general sigmoid pattern paralleled observed growth curves. The sigmoid pattern was generally improved and growth inflections were more apparent using the Quadratic Response Method. The Quadratic Response Method correctly predicted periods of negative or zero growth rate in Feed-1.

Average back-calculated lengths at age were paired with observed lengths to further evaluate the relative performance of the methods (Fig. 8). Deviations from observed lengths were substantially less for the Quadratic Response Method than for either the Simple Regression Method or Biological Intercept Method (Fig. 8). The Biological Intercept Method showed a positive bias at small larval lengths and a negative bias at greater larval lengths. The Simple Regression Method did not show bias for small larvae, but variance about the slope was not improved over the Biological Intercept Method. The Quadratic Response Method resulted in little deviation of back-calculated lengths from those observed and the best fit of data.

TABLE 3. Somatic growth rates by feeding regimes. Experimental broods are combined for each regime.

Feeding regime	SL vs. age				
	Intercept	Slope	SE, slope	N	R ²
Feed-1 (delayed 10 d)	4.89	0.033	0.0050	188	0.19
Feed-2 (delayed 6 d)	3.34	0.23	0.0067	234	0.84
Feed-3 (fed low concentration)	4.53	0.16	0.0079	211	0.67
Feed-4 (fed medium concentration)	3.69	0.27	0.0072	236	0.86
Feed-5 (fed high concentration)	3.06	0.38	0.0083	240	0.90
Pens	3.97	0.23	0.014	126	0.70

TABLE 4. Coefficients for regression-based back-calculation models. Laboratory data ($N = 955$) were fit with linear, multiple, and quadratic regression models. Pen data ($N = 118$) were fit with only a multiple regression model. Selection of predictors in regression was based on a forward stepwise regression procedure. Int = intercept; Diam = otolith diameter (μm).

Int	Diam	Age	Diam·age	Diam·diam	Age·age	R ²
<i>Laboratory-reared larvae</i>						
4.16	0.0239	—	—	—	—	0.917
3.11	0.0410	0.0530	-0.000867	—	—	0.935
4.83	0.0627	-0.357	-0.00254	0.0000334	0.0184	0.952
<i>Pen-reared larvae</i>						
4.69	0.0214	—	-0.000386	—	—	0.933

TABLE 5. Partial sum of squares (SS) for predictors in the Multiple Regression Method and Quadratic Response Method.

Factor	SS	df	F	P
<i>Laboratory-reared larvae: Multiple Regression Method</i>				
Diameter	3156.3	1	15444.3	0.0001
Age	5.9	1	29.1	0.0001
Otolith diameter·age	54.4	1	266.3	0.0001
Model	3216.7	3	5246.6	0.0001
Residual	194.3			
<i>Laboratory-reared larvae: Quadratic Response Method</i>				
Diameter	3156.3	1	20118.8	0.0001
Age	5.9	1	37.8	0.0001
Diameter·age	54.4	1	346.9	0.0001
Diameter·diameter	4.3	1	27.3	0.0001
Age·age	41.2	1	262.5	0.0001
Model	3262.1	5	4158.7	0.0001
Residual	148.9			
<i>Pen-reared larvae: Multiple Regression Method</i>				
Diameter	119.3	1	1590.1	0.0001
Otolith diameter·age	2.1	1	28.2	0.0001
Model	121.4	2	809.2	0.0001
Residual	8.6			

Pen Confirmation

Larvae from pen-rearing experiments contained otoliths which were relatively larger than larvae reared in tanks (Fig. 9). A difference between otolith growth between laboratory and "natural" fish has been noted in the literature (Hovenkamp 1990), but the magnitude of the difference was unexpected. Pen-reared larvae grew at rates similar to tank-reared larvae subjected to the Feed-3 feeding regime (Fig. 5; Table 3). However, otoliths averaged 18% larger for pen-reared larvae. This

difference caused the laboratory-derived Quadratic Response Method to substantially overestimate back-calculated lengths (Fig. 10). Despite this overestimate, the method correctly predicted growth inflections. The Biological Intercept Method accurately predicted average growth rate and identified an early growth inflection but tended to linearize other parts of the growth curves.

Age and otolith diameter information was available for the pen study and was used to calculate new coefficients for the

TABLE 6. Analysis of variance for the effect of age on residuals from the overall otolith versus fish length regression ($N = 955$). SS = sum of squares. *Age effect significant ($P < 0.0001$).

Feeding regime	Among ages			Within ages	
	SS	df	F	SS	df
Feed-1	43.00	5	116.6*	10.98	14
Feed-2	7.29	5	16.8*	17.43	20
Feed-3	16.12	5	27.3*	21.29	18
Feed-4	20.31	5	38.5*	21.10	20
Feed-5	28.80	5	54.2*	20.49	19

four different methods. No quadratic terms were significant and the Multiple Regression Method provided the best model fit (Tables 4 and 5). Methods applied to pen-reared larvae performed similarly to their application on tank-reared larvae (Fig. 10).

Discussion

Growth Effect

The continuous range of relative otolith size indicates that terms such as “uncoupling” or “decoupling” (Brothers 1981; Mosegaard et al. 1988; Wright et al. 1990) of otolith and somatic growth are probably inaccurate. results clearly demonstrate that the growth effect is observed when larvae and juveniles continue to grow, not just when growth ceases. We believe that otolith growth continuously scales to somatic growth but does so in an age-dependent manner.

Age effects occur not due to developmental events, or due to a gradual decline or increase in otolith growth in older fish, but due to the accumulation of days with respect to fish length. Otolith growth is a conservative daily process (Mugiya 1987; Mugiya and Oka 1991); some constant or proportional amount of calcification occurs onto the otolith despite daily fluctuations in somatic growth rate. This hypothesis was confirmed by laboratory experiments which showed that otolith growth was less sensitive to growth conditions and more affected by the accumulation of days “stored” within the otolith’s microstructure. In analysis of residuals, negative inflections indicated that age contributed relatively more to otolith size than did fish size. Thus, during periods of declining growth rate and growth stasis, negative residuals were observed. Indeed, Feed-1 residuals remained negative despite a positive growth inflection at age 16 due to the growth history (accumulated age effect) of the fish. Conceptually, it is easier to relate age to otolith dimension in the extreme case, where somatic growth ceases but otolith growth continues because it is a daily process. However, we believe that the age effect is important across all negative, static, and positive growth rates.

In past work, we have attempted to explain the observation that, on average, otolith growth must reflect somatic growth, since correlations exist between otolith size and fish size (Campana and Neilson 1985). Biological rationale was provided which linked anabolism to calcium uptake rates, serum concentration, and otolith deposition (Secor and Dean 1989). Research by Mugiya and Oka (1991) has confirmed links between anabolism (RNA/DNA) and calcium serum and deposition levels. Certainly, metabolism in general could also be related to increased rates of otolith growth (Mosegaard et al. 1988; Wright 1991). However, in most larval fishes, we believe that metabolism cannot proceed independently of anabolism for sustained periods.

The relationship between otolith growth and temperature (this study; Mosegaard et al. 1988; Hovenkamp 1990) has produced a general theory relating otolith growth with metabolism (Mosegaard et al. 1988; Wright et al. 1990). However, research on in vitro otolith growth has shown that otolith calcification was not metabolically regulated. Otoliths continued to grow in hypophysectomized goldfish (Mugiya and Odawara 1988). The extent of crystal growth within the accretion zone (sensu Mugiya 1987) might be related to physiochemical factors and therefore be dependent on the environment of the endolymph (Mugiya 1974; Mugiya and Uchimura 1989; Mugiya 1990). Results showing a positive relationship between otolith growth and temperature could be due to the kinetics of crystal growth alone. In summary, relating a temperature effect to our age effect, we believe that the range of daily increment growth is a conservative process and that minimum and maximum constraints are placed on increment widths through the interaction of the endogenous rhythm of calcification and matrix deposition (genetic and endocrinological control) with temperature (kinetics or growth-independent metabolism) and somatic growth (anabolism). Defining a set of experimental conditions to predict daily somatic growth rate from increment widths will therefore be very difficult.

Performance among Methods

The Quadratic Response Method and Multiple Regression Method provided the best estimates of back-calculated size at age for laboratory-reared larvae. The addition of age in the regression-based methods dramatically improved back-calculation precision. The inclusion of quadratic terms further weighted age effects and permitted greater “flexibility” in fitting curves to periods of negative growth.

The Biological Intercept Method and Simple Linear Regression Method averaged growth patterns, linearized growth inflections, and did not predict periods of tissue loss or growth stasis. Predicted lengths at age were not significantly different between the two methods. Campana (1990) predicted that when linear regressions were fit to data with values near the origin, average back-calculated lengths would be similar to the Fraser-Lee Method. Therefore, our results corroborate his prediction. Campana (1990) tested his method on simulated individual growth trajectories which contained a single growth inflection. The method showed a 42% deviation from the growth inflection point; the back-calculated growth curve contained less curvature than the curve derived from the simulated observations. In the current application of the Simple Regression Method and Biological Intercept Method, the conservative and linear otolith growth pattern was translated into back-calculated somatic growth curves which were relatively insensitive to growth transitions.

Campana (1990) showed in a simulation exercise that the growth effect could explain the Lee’s Phenomenon, where back-calculated sizes are smaller than observed size at age. Interestingly in this application, the modified Fraser-Lee Method overestimated size at age. The comparison of whole-otolith diameters (observed size) with digitized diameters (back-calculated size) (Fig. 3) indicated that there was no size-selective mortality during the experiment. Therefore, the method itself must be biased. Possible error can be ascribed to the definition of the Biological Intercept. For instance, very little fish growth occurred between 5 d (mean = 5.11 mm SL) and 7 d (mean = 5.42 mm SL) whereas otolith size increased an average of 12 μm between these ages. We have not deter-

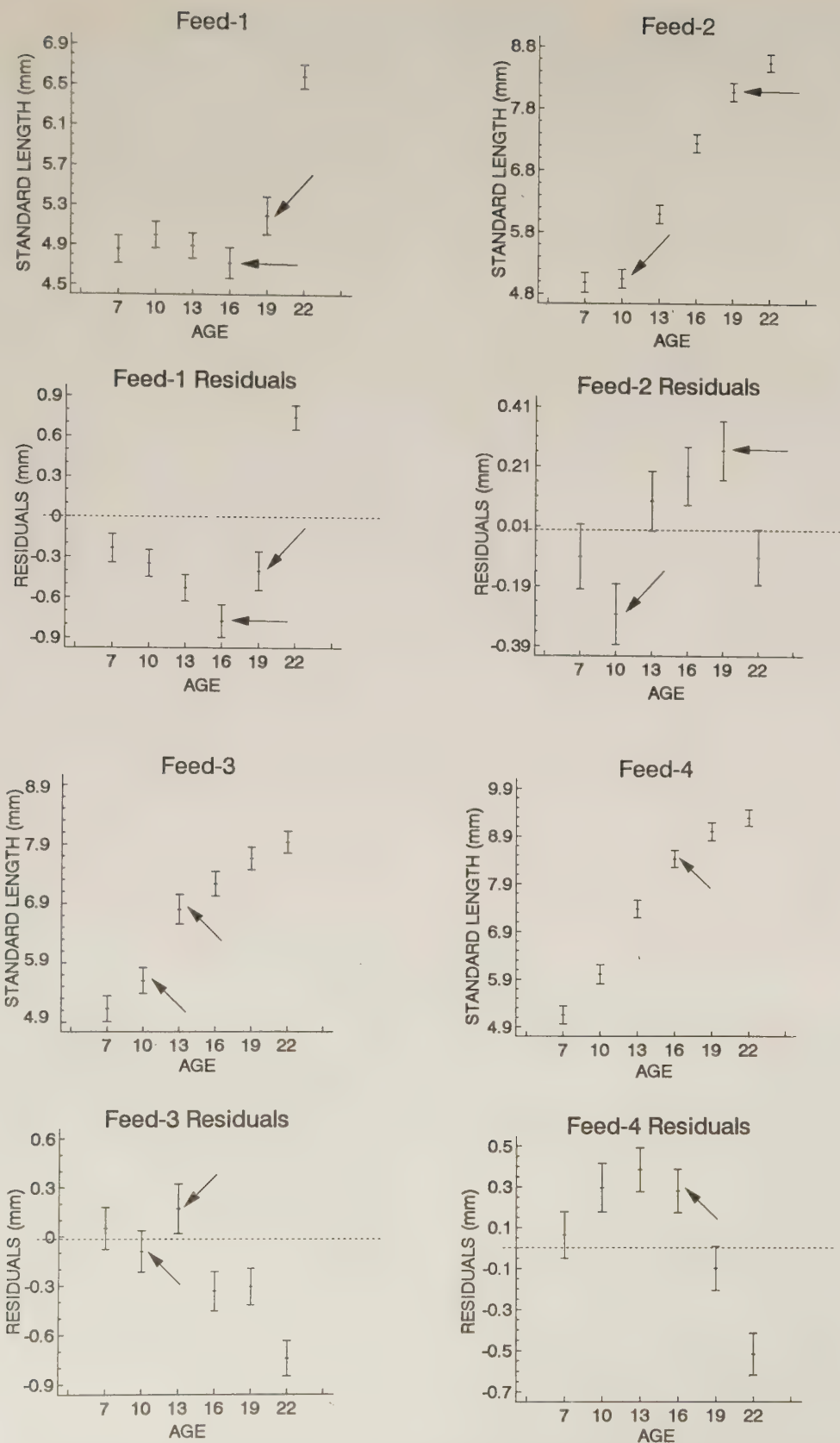
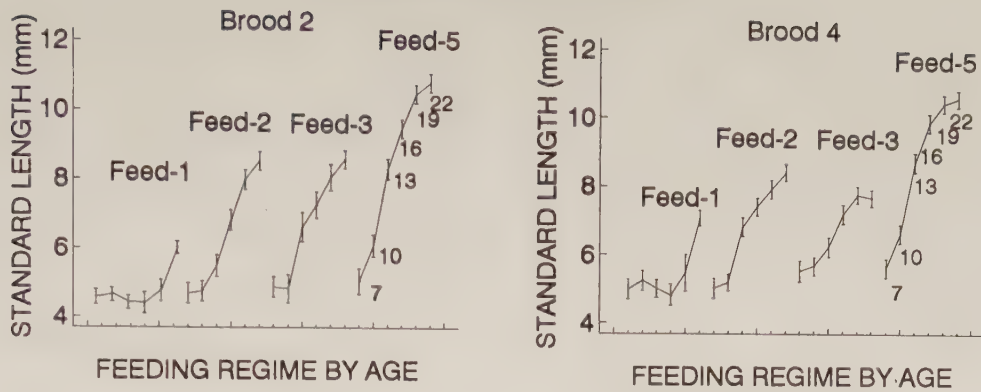
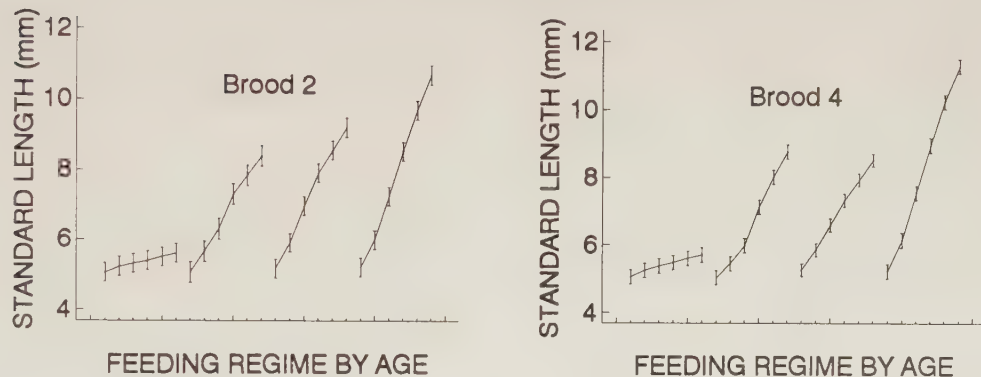


FIG. 6. Residual patterns across feeding regimes. Data have been combined across broods. Top panels show 95% confidence intervals for observed lengths at age. Bottom panels show residuals from the overall otolith diameter versus SL regression plotted against age. Broken line indicated regression line; arrows show growth inflections.

Observed Growth Rates



Simple Regression Method



Biological Intercept Method

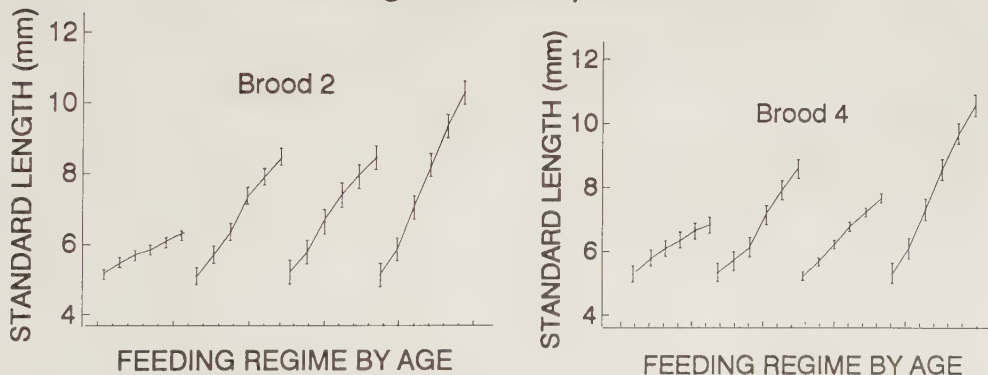


FIG. 7. Comparison of back-calculated lengths at age with observed lengths at age for tank-reared larvae. 95% confidence intervals for observed or back-calculated lengths are shown by feeding treatment and age. Each panel contains four growth curves, one for each brood. All broods are scaled similarly to the y-axis. Ages are listed below confidence limit bars only for the Feed-5 treatment of the observed length panels. The other broods follow this designation. (Fig. 7 concluded next page)

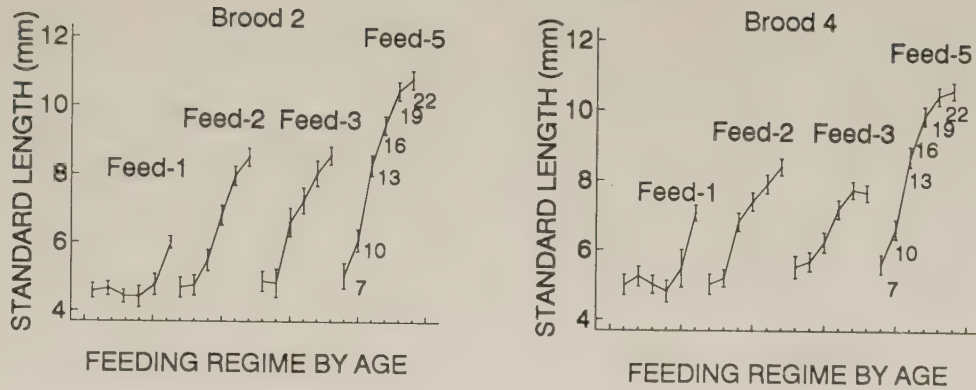
mined when “constant proportionality” begins and believe further experimental refinement of the Biological Intercept is necessary. Finally, because size-selective mortality did not occur, we could not compare its effect with Lee’s Phenomenon in back-calculation procedures.

An alternative method for time varying growth rates was given in Campana (1990) and used a parameter R , which is termed the “growth effect”, and is the slope of otolith size versus fish size regression slopes regressed on somatic growth rate. This slope has only been quantified for striped bass (Secor et al. 1989; Campana 1990, $R = 0.4$) and was linear in this instance. However, in the current application, the relationship

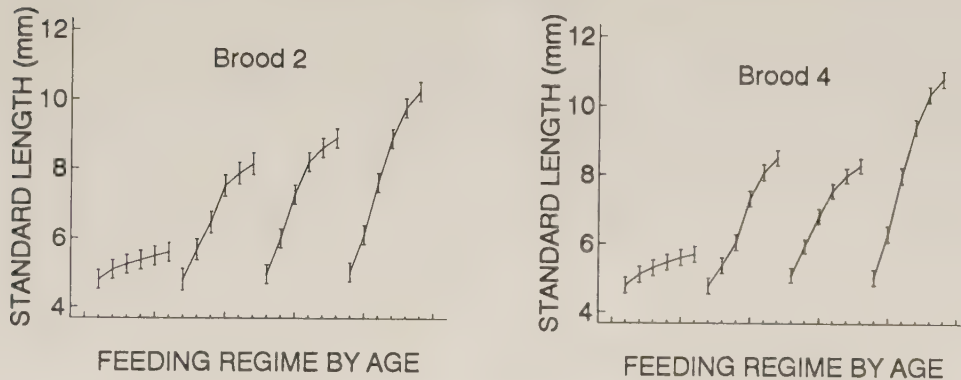
between relative otolith size and somatic growth rate was not linear and was less than that for juvenile striped bass ($R = 0.33$). In general, we do not expect that the R will be constant across species and life stages.

The application of regression-based back-calculation methods on pen-reared larvae failed to provide accurate predictions. The magnitude of the difference in otolith – fish length ratios between laboratory and pen studies resulted in overestimation of lengths at age. Growth and brood effects did not explain the difference in relative otolith size. However, pen-reared larvae experienced temperatures that averaged 5°C warmer than tank-reared larvae. A temperature effect would be consistent with

Observed Growth Rates



Multiple Regression Method



Quadratic Response Method

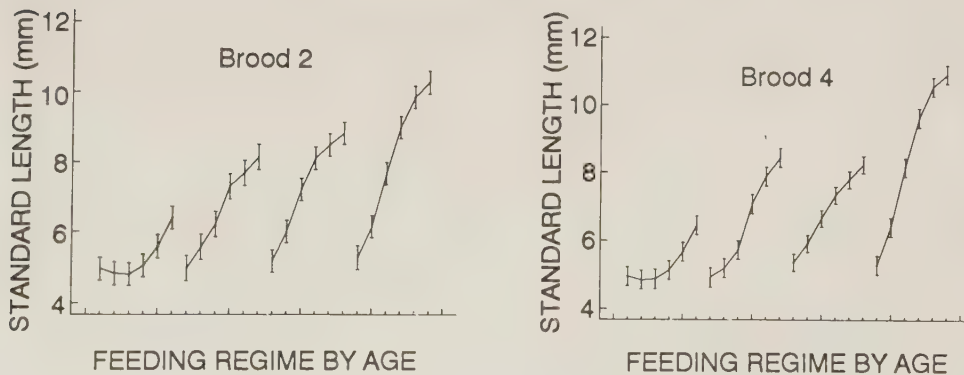


FIG. 7. (Concluded)

Mosegaard et al.'s (1988) findings that otolith growth is positively related to temperature, independent of somatic growth (see previous discussion). A second possible explanation are secondary environmental effects on daily otolith growth. Campana and Neilson (1985) have proposed that environmental rhythms other than the primary entrainer, photoperiod, can reinforce daily otolith growth. Since otolith growth is endogenously controlled, it is conceivable that secondary environmental "signals" (temperature, pH, food supply and quality, and turbidity) absent from the laboratory experiments could have increased the magnitude of daily otolith growth.

A major problem in the test on pen-reared larvae can be ascribed to the nature of regression analysis itself. The ability to make predictions is dependent on the range and distribution of data within the regression. For instance, when regressions

were fitted to pen data, age main effects and quadratic terms were not significant. This may have been due to a restricted range of growth rates (e.g. if individual growth rates were all identical, no growth effect would occur). In laboratory experiments, we have produced extremes in the range of possible growth rates for larval striped bass and these might not be represented in the field situation. Differences in the distribution of growth rates and environmental conditions among possible field applications require that the development and application of regression-based methods proceed for the same experimental population.

Despite the failure of the test, we have provided experimental proof and biological rationale for the inclusion of age in regression-based back-calculation methods. Additionally, the ability of the laboratory-derived Quadratic Response Method to cor-

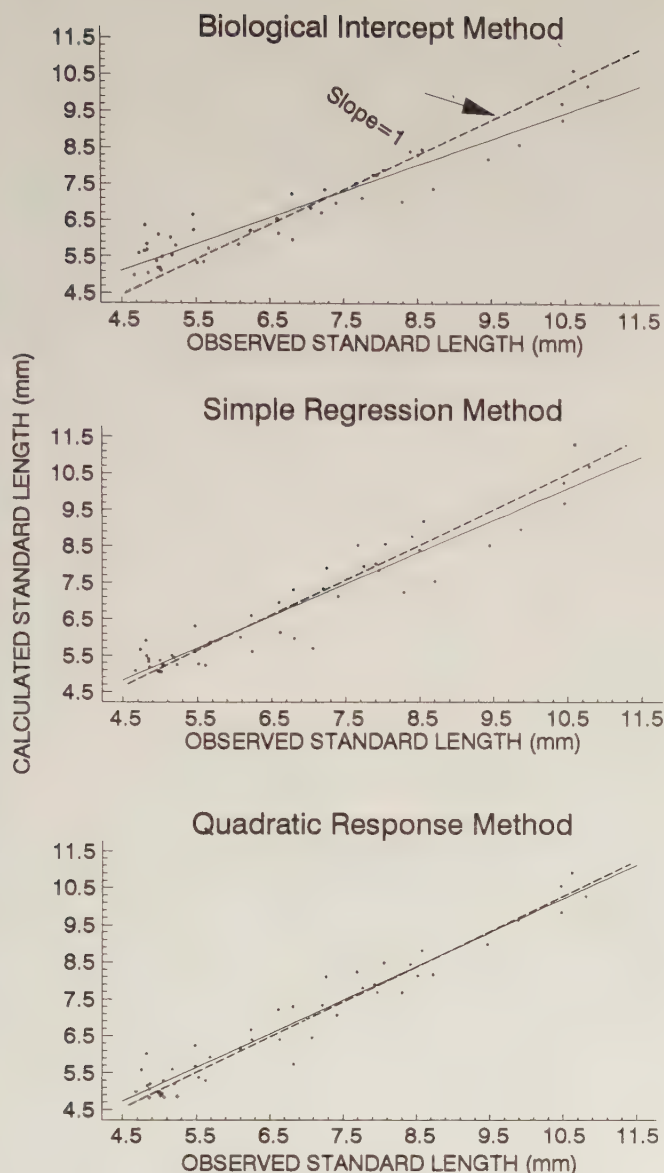


FIG. 8. Observed SL versus back-calculated SL for the Biological Intercept Method, Simple Regression Method, and Quadratic Response Method. The Multiple Regression Method showed similar results to the Simple Regression Method and is not shown in this demonstration. Solid lines indicate regression lines; broken lines indicate slope = 1 (expected fit). Biological Intercept Method: $1.796 + 0.745 \cdot \text{SL}$; $N = 48$, $R^2 = 0.889$. Simple Regression Method: $0.860 + 0.880 \cdot \text{SL}$; $N = 48$, $R^2 = 0.902$. Quadratic Response Method: $0.592 + 0.919 \cdot \text{SL}$; $N = 48$, $R^2 = 0.941$.

rectly predict growth inflections in pen-reared larvae supports using age as a predictor. These findings and concepts verify the approach of previous studies in predicting age based on relative otolith dimension for juveniles (Secor and Dean 1989) and adults (Boehlert 1985; Radtke et al. 1985; Radtke et al. 1989).

Field Applications

Because of the extensive field data required to apply regression methods, their applications may be limited. Since relative

otolith dimension has been related to growth rate, ontogeny, temperature, location, and genetics, we have recommended that Simple Regression Methods be used only in situations where they were developed (Secor and Dean 1989). Similarly, more complex regressions which use age should be developed for each field application. Data required comprise larval lengths and ages over the temporal and spatial range of the population studied. This information is already available for some historic surveys. For instance, where spawn dates have been back-calculated from larvae, information on age at length and otolith size is already known. These data can be used to construct an otolith growth model based on the interaction of age and otolith size. Incorporation of temperature records (Mosegaard et al. 1988) could further improve prediction.

Application of these regression methods begs the question, if fish length at age is already known over the period the investigator wishes to back-calculate, then why use back-calculation procedures at all? Our response is that these procedures can provide detailed information on individual growth histories whereas size at age distributions quantify only population averages. Issues in recruitment research have recently focused on individual processes of fish, their growth and fate, processes which are size specific (Anderson 1988; Miller et al. 1988; Beyer 1989). By investigating the otolith microstructure of survivors, size-selective mortality can be quantified among life stages. For instance, when during the early life history does size-selective mortality predominate?

There are many situations where the Quadratic Response Method or Multiple Regression Method cannot be applied or where application is unwarranted. For instance, data on larval length, otolith size, and age may be lacking or biased or information will only be needed on average past growth rates. Campana's (1990) Biological Intercept Method will have valuable applications in such cases. The method is much easier to apply than regression methods and can provide unbiased and accurate mean back-calculated growth rates. However, it will be imprecise and biased where growth inflections or negative growth occur. An important criterion for the Biological Intercept Method will be that back-calculated lengths are not too far out of the range of the fish's length at capture. For instance, due to the effect of ontogeny on relative otolith size (Rosenberg and Haugen 1982; Wilson and Larkin 1982; Campana 1984; Volk et al. 1984; Rice et al. 1985; West and Larkin 1987; Secor et al. 1989), it will be impractical to use juvenile or adult otoliths in the back-calculation of larval growth rates by this method.

Pannella (1971) hypothesized that the crystals and protein of otoliths contained information on fish age, daily growth, and temperature. However, an important consideration is that otoliths occur within sacs of endolymph distant from the cellular processes associated with anabolism. This isolation imposes difficulties in experimentally relating anabolism to otolith growth. Thus, current theory on otolith growth remains speculative. However, indirect correlations have commonly documented positive relations between otolith and somatic growth rate (Secor and Dean 1989). In this report, those correlations were used to determine the best method for back-calculating fish size from otolith microstructure. Because daily otolith growth has been found to be conservative relative to somatic growth in several studies (this study; Volk et al. 1984; Bradford and Geen 1987; Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; Secor et al. 1989; Wright et al. 1990), investigators should be cautious about the amount of growth information interpretable from single daily increments.

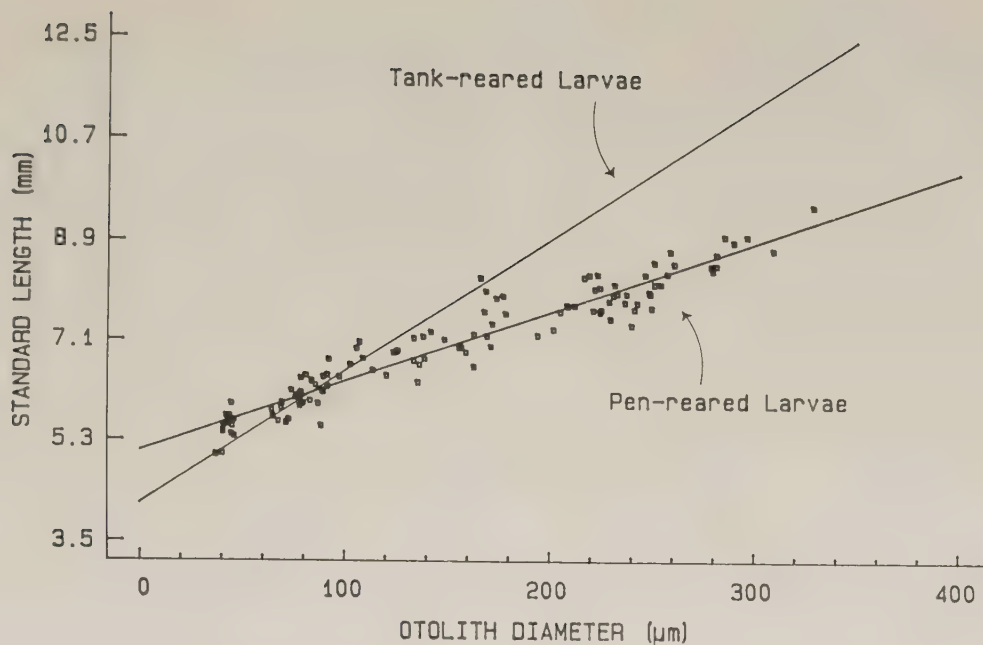


FIG. 9. Relationship between SL and otolith diameter for pen-reared larvae. Regression line for tank-reared larvae is indicated. $SL = 5.010 + 0.0127 \cdot \text{otolith diameter}$; $N = 118$, $R^2 = 0.917$.

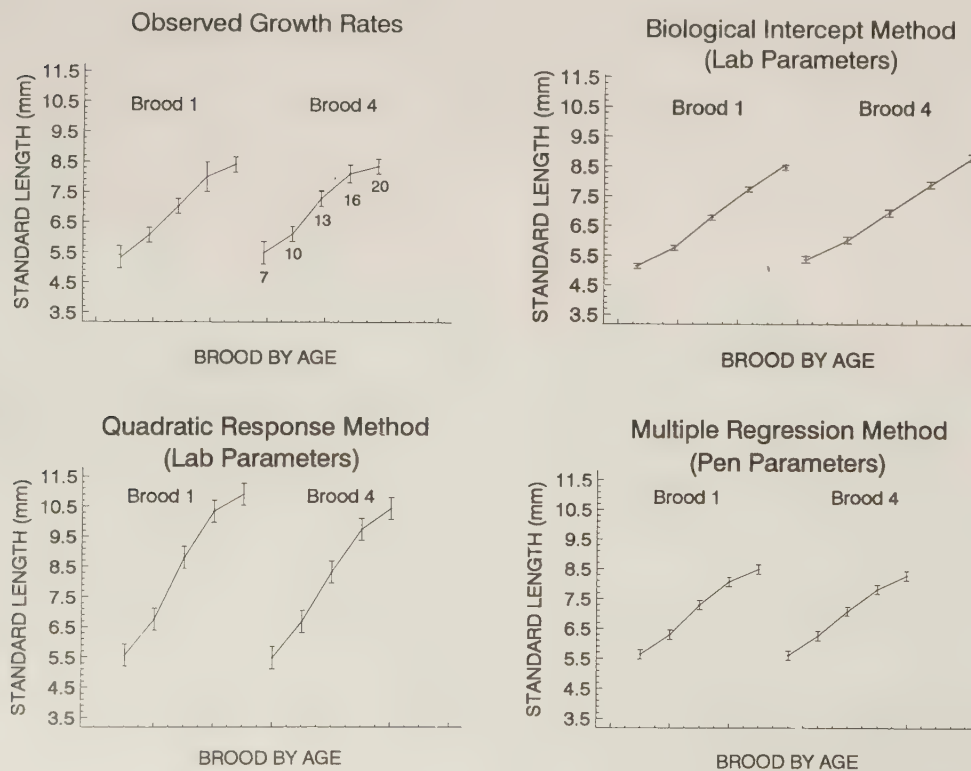


FIG. 10. Comparison of back-calculated lengths at age with observed lengths at age for pen-reared larvae. Three back-calculation procedures are shown. The Biological Intercept Method and Quadratic Response Method were parameterized based on laboratory data; the Multiple Regression Method was parameterized based on data from pen-reared striped bass (see Table 5). 95% confidence intervals for observed or back-calculated lengths are shown by brood and age. Each panel contains two growth curves, one for each brood. All broods are scaled similarly to the y-axis. Ages are listed below confidence limit bars only for brood B4 of the observed length panel. The other broods follow this designation.

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Grazing by Zooplankton and Its Relationship to Community Structure

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Zooplankton can consume a substantial portion of the phytoplankton, but grazing rates are notoriously variable seasonally and among sites. We developed models relating grazing rates to characteristics of zooplankton communities, food concentration, and water temperature. Grazing rates were measured in 30 zooplankton communities that differed in biomass, size distribution, and taxonomic composition. Crustaceans grazed per day 2–21% of the chlorophyll in algae <35 μm , which is within the range of most grazing rates measured in other studies. Grazing rates were positively related to zooplankton biomass and negatively related to food concentration, although much variation among communities remains unexplained ($R^2 = 0.19\text{--}0.35$). Surprisingly, we could not detect a general relationship between zooplankton size distribution and grazing rate. Communities dominated by large zooplankton (mostly *Daphnia* and *Diaphanosoma*) did not tend to have higher grazing rates than communities dominated by small zooplankton. Zooplankton taxonomic composition was significantly related to grazing rates but explained little variation among communities. Grazing rates calculated from published allometric equations were biased, usually overestimating phytoplankton removal by zooplankton.

Le zooplancton peut consommer une partie appréciable du phytoplancton, mais il est bien connu que les taux de broutage varient beaucoup entre les saisons et les lieux. Nous avons élaboré des modèles établissant des relations entre les taux de broutage et certaines caractéristiques des communautés zooplanctoniques, la concentration de nourriture et la température de l'eau. Les taux de broutage ont été mesurés dans 30 communautés zooplanctoniques différant de par la biomasse, la répartition des tailles et la composition taxinomique. Les crustacés brouaient par jour 2 à 21% de la chlorophylle des algues de tailles inférieures à 35 μm ; ces valeurs se situent dans la gamme des taux de broutage mesurés par d'autres chercheurs. Les taux de broutage présentaient une corrélation positive avec la biomasse zooplanctonique et une corrélation négative avec la concentration de nourriture, mais la plus grande partie de la variation entre les communautés demeure inexpliquée ($R^2 = 0,19\text{--}0,35$). Nous avons été surpris de ne pouvoir déceler de relation générale entre la distribution des tailles du zooplancton et leur taux de broutage. Les communautés dominées par de gros organismes zooplanctoniques (surtout des *Daphnia* et des *Diaphanosoma*) n'avaient pas tendance à présenter des taux de broutage supérieurs à celles où dominaient les petits organismes zooplanctoniques. La composition taxinomique présentait une relation significative avec les taux de broutage, mais expliquait très peu la variation entre les communautés. Les taux de broutage calculés à partir des équations allométriques publiées étaient biaisés et surestimaient généralement la consommation du phytoplancton par le zooplancton.

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Zooplankton grazing can be a major source of phytoplankton mortality, altering both the biomass and composition of algal communities (Porter 1977; Reynolds 1984; Sterner 1989). Grazing, however, is notoriously variable, both in space and in time. The importance of grazing varies with depth and time of day (Haney 1973; Lampert and Taylor 1985; Mourcelatos et al. 1989), across seasons (Haney 1973; Gulati et al. 1982; Thompson et al. 1982; Hart 1986), and among lakes (Haney 1973; Gliwicz 1969; Bleiwas and Stokes 1990). Although many studies have focused on the factors affecting

the grazing of individuals (Peters 1984; Peters and Downing 1984), we know less about the variables related to the grazing rates of communities (Gulati et al. 1982; Hart 1986).

Grazing rates are expected to vary with the biomass, size structure, and taxonomic composition of different zooplankton communities. Within lakes, community grazing rates increase with zooplankton biomass (Gulati et al. 1982; Hart 1986). We expect this relationship to hold among lakes as well. Grazing rates should also be related to the size of organisms in a community, although different lines of evidence for this effect give different predictions. Allometric equations show that small organisms graze more per unit biomass than large organisms (Peters and Downing 1984; Jarvis et al. 1988, using length–

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weight relationship from Peters and Downing 1984; but see Chow-Fraser and Knoechel 1985; Knoechel and Holtby 1986), suggesting that for a given biomass, communities dominated by small zooplankton should graze more than communities dominated by large organisms. The cascading trophic interaction hypothesis, on the other hand, is based on the importance of large cladocerans (mainly *Daphnia*) as key grazers (Hrbáček et al. 1961; Shapiro 1980; Carpenter et al. 1985) and predicts that communities dominated by large zooplankton should graze more than communities dominated by small organisms. Taxonomic composition of a community should also be important. Different cladoceran taxa have similar grazing rates once body size is taken into account (Chow-Fraser and Knoechel 1985; Knoechel and Holtby 1986), but copepods feed at lower rates than cladocerans (Peters and Downing 1984; Knoechel and Holtby 1986). Given equal biomass, communities dominated by copepods are, therefore, expected to graze less than those dominated by cladocerans. It is usually assumed that the biomass, size structure, and taxonomic composition of zooplankton communities affect their impact on phytoplankton. These notions, however, remain to be tested across a broad range of communities.

Zooplankton grazing rate also varies with environmental factors. Studies of individual taxa and of communities suggest that zooplankton grazing rate is affected by food concentration, food quality (algal size, shape, taste, nutrient content), high turbidity, and water temperature (Gulati et al. 1982; Peters 1984; Hart 1988).

Community grazing rates are difficult to measure, due in part to their variation with depth and time of the day. There have been attempts to estimate grazing rates from average literature values (Forsberg 1985) or from empirical allometric models (Siegfried 1987; Leavitt and Carpenter 1990; Vanni and Findlay 1990). Allometric equations are used to predict the grazing rate of an individual from its body size, and the contribution of all organisms is added to estimate community grazing rate (Knoechel and Holtby 1986). Allometric equations have also been used to model grazing rates and compare their importance among zooplankton communities (Carpenter and Kitchell 1984). Several allometric models have been proposed: Peters and Downing (1984) summarized laboratory measurements from different studies, and Chow-Fraser and Knoechel (1985) and Knoechel and Holtby (1986) based their models on in situ grazing rates from several cladoceran species. Other equations exist (e.g. Burns 1969; Kibby and Rigler 1973; Mourelatos et al. 1989) but are limited to one or a few closely related taxa. Most allometric equations are based on rates measured by feeding zooplankton one or a few types of radioactively labeled particles. Several authors have warned that rates measured on one type of food particle cannot be extrapolated to algal communities (Gliwicz 1969; Lampert 1988; Mazumder et al. 1990). If allometric models are to be used to estimate the removal of phytoplankton by zooplankton, it is important to compare predictions with grazing rates measured on whole algal communities.

We are interested in quantifying and predicting the magnitude of zooplankton herbivory across systems. We measured the grazing rates of communities that differed in biomass, size structure, and taxonomic composition, both within lakes through time and across lakes. We then developed models relating grazing rates to characteristics of zooplankton communities and to environmental parameters. Finally, grazing rates predicted from allometric equations were tested against direct measurements for a wide range of zooplankton communities.

Methods

We sampled 30 zooplankton communities from 16 lakes in New York, Connecticut and Pennsylvania, USA, from September to October 1988 and April to October 1989. Communities sampled from the same lake were taken approximately 1 mo apart. We measured grazing rate, zooplankton biomass, size distribution, and taxonomic composition of zooplankton, food concentration, and water temperature.

In situ Community Grazing Rate

Community grazing rate was measured in situ, on the natural phytoplankton assemblage, using a technique developed by Lehman (1980) and Lehman and Sandgren (1985). Ten to fifteen 21-L clear polyethylene cubitainers were filled with lake water pumped from 1–2 m depth and filtered through a 73- or 80- μm mesh net to remove macrozooplankton. Zooplankton were then added to each enclosure in different concentrations. The range of concentrations used varied among communities, usually not exceeding five times natural density. Zooplankton were concentrated by pumping a known volume of water (21 L for 1 $\times$, 42 L for 2 $\times$, etc.) from 1–2 m into an immersed plankton net (73 or 80 μm), using a constant flow bilge pump (0.57 L $\cdot$ s $^{-1}$). This gentle filtration method reduced zooplankton crowding until the complete sample was concentrated in the cod-end of the plankton net and quickly transferred to the assigned enclosure (<60 s). The zooplankton was dispensed to different enclosures with good precision (SE/mean of in situ biomass < 0.15). Nutrients were added to each enclosure to raise ambient concentrations by 14–15 μM NH_4NO_3 and 1–1.5 μM KH_2PO_4 in order to saturate algal growth. In six different manipulations, we checked that doubling this level of nutrient addition did not further increase algal growth (one-tailed *t*-test, all *P* > 0.25). The containers were closed, excluding as much air as possible to minimize the area of air–water interface where *Daphnia* and *Bosmina* tend to get caught, and were mixed thoroughly. All but one manipulation (Upton 5) were set up at night to take advantage of the high density of zooplankton close to the surface and to avoid light shock to the invertebrates. We are assuming that diel variations in grazing rate are not inherent to the organisms but are due to changes in zooplankton communities, phytoplankton assemblages, and environmental variables and, consequently, that models developed for nighttime surface zooplankton can be applied to other zooplankton communities. The containers were incubated in the lake at 1.5 m depth for 23–37 h. Our manipulations were shorter than most past in situ applications of this method where the net effect of zooplankton grazing and nutrient regeneration was studied (3–4 d; Lehman and Sandgren 1985; Bergquist and Carpenter 1986). Our goal was to measure grazing rate while minimizing changes in bacteria, algae, and zooplankton in the enclosures.

In each manipulation, the algae are assumed to grow at equal rates in all enclosures (ensured by nutrient addition) but to be grazed at different rates depending on the density of zooplankton. Grazing rate (per day) is, therefore, the slope ($|b|$) of the equation

$$(1) \quad r = b(\text{ZC}) + A$$

where *r* is the realized algal growth rate (per day), ZC is zooplankton concentration ($\times$ natural density), and *A* is the realized algal growth when saturated with nutrients in the absence of macrozooplankton (per day). The coefficients of this equation (*A*, *b*) were estimated by simple linear regression. Con-

tainers where algal growth rate differed by more than 3 standard deviations from the average relationship were considered to have a disproportionate influence on b (Draper and Smith 1981) and were excluded from the calculations. About 10% of the enclosures were discarded (32 of 336 enclosures). In each zooplankton community, 8–15 enclosures were used to estimate grazing rates.

Realized algal growth rate

Realized growth rate (r) was measured from changes in chlorophyll concentrations during the manipulation. Water from each enclosure was collected at the beginning and at the end of the manipulation and was filtered through a 35- μm Nitex mesh. The filter removed algae $>35\ \mu\text{m}$ in two or three dimensions, many of which are not eaten by zooplankton (Gliwicz 1977; Vanderploeg 1981; Vanderploeg et al. 1988). The filtrate retained the edible portion of the algal community, consisting of algae smaller than 35 μm and some algae longer than 35 μm . Two subsamples of the filtrate were filtered through GF/F filters and frozen. The samples were ground, the chlorophyll extracted 14–20 h in basic methanol (2 mL of 0.5 M NaOH per litre of methanol) and read on a Turner model 10 fluorometer (method modified from Holm-Hansen and Riemann 1978). Phaeopigment:chlorophyll concentration ratios changed during the manipulations but these changes were usually of similar magnitude across the zooplankton biomass gradient and did not, therefore, affect grazing rate calculations (comparison of slopes for phaeopigment:chlorophyll concentration ratio versus zooplankton biomass at the beginning and at the end of the manipulation; 11 of 12 manipulations with $P > 0.05$). In Upton 2, changes in phaeopigment:chlorophyll concentration ratios increased with zooplankton biomass, but the phaeopigment:chlorophyll ratios were small and therefore did not affect b in equation 1. No phaeopigment correction was necessary because grazing rates calculated from corrected and uncorrected chlorophyll values were not statistically different (F -tests for differences among slopes of equation 1 in 12 manipulations, all $P > 0.25$; Sokal and Rohlf 1981, p. 499). Realized algal growth rate (r , per day) was calculated as

$$(2) \quad r = \ln(C_1/C_0)/T$$

where C_0 and C_1 are chlorophyll concentrations (micrograms per litre) in algae $<35\ \mu\text{m}$ at the beginning and at the end of the manipulation, respectively, and T is the time period (days) over which grazing is measured. The realized growth rates measured in each enclosure were used in equation 1 to calculate zooplankton grazing rate.

In two manipulations (Upton 1 and Tyrrel 1), we also measured the realized growth rate of cryptomonads. The algae were sampled from four to five enclosures at the beginning and at the end of each manipulation and preserved in Lugol's solution (American Public Health Association et al. 1985). We counted cryptomonads in subsamples using a Sedgwick–Rafter chamber until a minimum of 100 cells were counted. Enclosures with three times in situ zooplankton densities or more had to be discarded because of saturation in the removal of cryptomonad cells. Grazing rate on cryptomonads was, therefore, measured as the disappearance of cells in three enclosures containing between zero and two times natural zooplankton densities. Realized cryptomonad growth rate (r) was calculated from direct cell counts using equation 2, where C_0 and C_1 are number of cells per litre.

Conversion of grazing rate to other units

For comparison with other studies, grazing rates had to be converted to different units. Grazing rates in litres per milli-

gram dry weight per day are the quotients of rates in per day units and zooplankton biomass (milligrams dry weight per litre). Percent algae grazed per day is calculated as $((1 - e^b)/100)$ where b is the slope in equation 1.

Composition of Zooplankton Communities

Zooplankton biomass

Crustacean biomass (including nauplii) was measured in three to eight enclosures per manipulation. The zooplankton was collected on a 73- μm -mesh filter at the end of each manipulation, anesthetized with carbonated water, and preserved in 4% sucrose-formaldehyde (Prepas 1978). All crustaceans were counted in samples containing fewer than 2000 organisms, and when counts in subsamples did not conform to a Poisson distribution (Elliott 1977). Otherwise, subsamples were taken until at least 400 organisms of the most common taxon were counted. When available, 30–50 organisms per taxon were measured. Body lengths were measured at $100\times$ magnification (nonnaupliar calanoids and cyclopoids, *Daphnia*, *Diaphanosoma*, and *Holopedium*) or $250\times$ magnification (*Bosmina*, *Ceriodaphnia*, *Chydorus*, and nauplii) using an image analysis system. *Daphnia* with helmets were measured from the base of the spine to the center of the eye (L_E) and their length multiplied by 1.16 to estimate total body length (L_T) (average ratio $L_T:L_E$ of 83 nonhelmeted *Daphnia* from three different communities, SE = 0.005). Body lengths were transformed to dry weights using equations from Bottrell et al. (1976) for *Bosmina* spp., *Ceriodaphnia quadrangula*, *Daphnia* spp., *Diaphanosoma brachyurum*, cyclopoids, and *Diaptomus gracilis*, Rosen (1981) for *Chydorus sphaericus*, Lawrence et al. (1987) for *Holopedium gibberum*, and correcting for detransformations as suggested by Bird and Prairie (1985).

Zooplankton biomass was calculated by adding the predicted dry weights of all individuals found in an enclosure. Total biomass was then divided by the zooplankton concentration factor (e.g. $0.5\times$, $1\times$, $2\times$) used in each enclosure to obtain in situ zooplankton biomass. The error around this estimate is calculated from replicate enclosures and does not include prediction errors from the length–weight equations.

Size distribution and taxonomic composition

Crustacean size distribution and taxonomic composition were estimated concurrently with biomass in three to eight enclosures per manipulation. Six variables were measured to represent different aspects of the size distribution of invertebrates in a community. We calculated the mean, median, variance, and skewness of the distribution in size (dry biomass in micrograms) of organisms. The Elser et al. (1987) coefficient (ZM_B), which is a measure of mean size weighted by the biomass of each taxon instead of its abundance, was calculated as

$$(3) \quad ZM_B = \sum_i (b_i \cdot m_i)/B$$

where b_i is the biomass of species i (milligrams per litre), m_i is the average individual weight of species i (micrograms dry weight), and B is total zooplankton biomass (micrograms per litre). We also considered the slope of a $\log_2$ – $\log_2$ relationship between density and individual body size (classified in intervals of $0.5 \cdot \log_2$ (dry weight)). This last index is a modification of the normalized size distribution used by Sprules and Munawar (1986) and is similar to the index used by Pace (1984) except that we used the frequency of individuals in each size class regardless of their taxonomic affiliation.

Taxonomic composition is quantified as the biomass of each major taxon: *Bosmina*, calanoids, cyclopoids, and *Daphnia*. Other taxa were found in less than half of the communities and were not considered in the analysis.

Environmental Parameters

Food concentration, lake trophy, and water temperature were usually measured at the beginning of the manipulation. Three 500-mL water samples were collected from 1–2 m depth with a bilge pump. Two aliquots per sample were passed through a 35- μ m Nitex mesh to remove large algae and two aliquots were left intact. All aliquots were filtered on GF/F filters and frozen. Chlorophyll was measured as described above. Chlorophyll concentration of algae <35 μ m is used as a measure of food concentration. Total chlorophyll concentration is a measure of lake trophy. Water temperature was measured with a YSI model 57 probe at 1 m depth.

Model Testing

We sought relationships between grazing rate ($|b|$ in equation 1) and characteristics of the zooplankton communities (biomass, size distribution, and taxonomic composition) and of the environment (food concentration and temperature). Four models were tested (Table 1) for all communities and for communities dominated by small zooplankton. Only model 1 (Table 1) was tested for communities dominated by *Daphnia* and *Diaphanosoma*, due to high correlation between ZB and SZB, B_D , B_{Cl} ($r^2 = 0.94$ – 0.99). The coefficients (b_n) were fit by multiple regression analysis, using backward and forward stepwise procedures. Grazing rates, zooplankton biomass, indices of zooplankton size distribution, and chlorophyll concentrations were transformed to logarithms (base 10) to fulfill the normality and homoscedasticity assumptions of regression analysis (Sokal and Rohlf 1981). We selected the model with adequate residuals that had the highest adjusted R^2 . A significance level of $\alpha = 0.05$ was used in all analyses. Models 1 and 2 in Table 1 test the effect of all variables, except taxonomic composition. Models 3 and 4 test the effect of zooplankton taxonomic composition on grazing rate. When at least one coefficient (b_n) associated with B_D , B_{Ca} , B_{Cy} , B_B , B_{Cl} , or B_{Co} in models 3 and 4 is different from zero, we conclude that the taxonomic composition of zooplankton communities has a statistically significant effect on its grazing rate. All analyses were performed on PC-SAS (version 6.03).

Predicted Community Grazing Rates

Zooplankton community grazing rates predicted from published allometric models were compared with measured rates. We tested the predictions from three equations as follows. (1) Peters and Downing's (1984) zooplankton model (equation 2, p. 769). The independent variables were either measured (body weight, food concentration, and duration of the measurement) or set to the median values for the model (food particle volume and container volume). Adult and copepodite cyclopoids were not considered. (2) Chow-Fraser and Knoechel's (1985) cladoceran model (equation 1, p. 571). Nonnaupliar calanoids were assigned a grazing rate of $2 \text{ mL} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$, the mean value measured by Chow-Fraser (1986, calculated from fig. 1, $n = 104$). Copepodite and adult cyclopoids were assumed not to feed on phytoplankton. (3) Knoechel and Holtby's (1986) cladoceran model (equation 2, p. 6). As was done by the authors, calanoids were assigned a grazing rate of $2 \text{ mL} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ and cyclopoids were not considered. Using each model, community grazing rate (CGR) was calculated from individual predictions as

$$(4) \text{ CGR} = \sum_j \sum_i ((n_j/m_j) \cdot \text{GR}_{ij})$$

where n_j is the number of invertebrates of taxon j present in a sample, m_j is the number of invertebrates of taxon j that were sized, and GR_{ij} is the grazing rate predicted for each measured individual i of taxon j . Community grazing rate was predicted for each replicate zooplankton sample and averaged.

Results and Discussion

We sampled 30 zooplankton communities (Table 2) in 16 lakes of different trophy (total chlorophyll concentration = 0.8 – $70.5 \mu\text{g} \cdot \text{L}^{-1}$), food concentration (chlorophyll in algae <35 μ m = 0.3 – $40 \mu\text{g} \cdot \text{L}^{-1}$), and temperature (12 – 25°C). Zooplankton biomass ranged from 0.03 to $1.24 \text{ mg} \cdot \text{L}^{-1}$ and the mean weight of crustaceans in these communities varied almost 20-fold (0.4 – $7.9 \mu\text{g}$). The communities also differed in taxonomic composition, some being very diverse (e.g. Tyrrel 5, West Branch), while others were dominated by one taxon (e.g. Waynewood, Upton 6, and East Twin with, respectively, 97, 95, and 91% of the biomass as *Daphnia*, Stilwell with 89% of the biomass as cyclopoids).

The grazing rate of each zooplankton community was measured as the change in realized algal growth rate (r) with increasing zooplankton concentration (Fig. 1). In contrast with the

TABLE 1. Models tested in search of predictive equations for zooplankton grazing rate (GR, d^{-1}). ZB is zooplankton biomass ($\text{mg} \cdot \text{L}^{-1}$), SD are indices of community size distributions including mean, median, variance, skewness, Elser et al. (1987) coefficient, and slope of normalized size distribution (see Methods, Composition of Zooplankton Communities; the first four indices were transformed to their logarithm base 10, while the last two were left untransformed), C35 is the concentration of chlorophyll in algae <35 μ m ($\mu\text{g} \cdot \text{L}^{-1}$), T is water temperature at 1 m depth ($^\circ\text{C}$), SZB is zooplankton biomass excluding adult and copepodite cyclopoids ($\text{mg} \cdot \text{L}^{-1}$), B_D is *Daphnia* biomass ($\text{mg} \cdot \text{L}^{-1}$), B_{Ca} is calanoid biomass ($\text{mg} \cdot \text{L}^{-1}$), B_{Cy} is cyclopoid biomass ($\text{mg} \cdot \text{L}^{-1}$), B_B is *Bosmina* biomass ($\text{mg} \cdot \text{L}^{-1}$), B_{Cl} is cladoceran biomass ($\text{mg} \cdot \text{L}^{-1}$), and B_{Co} is copepod biomass ($\text{mg} \cdot \text{L}^{-1}$).

Model	Equation
1	$\log_{10}(\text{GR}) = b_1 \log_{10}(\text{ZB}) + b_2 \text{SD} + b_3 \log_{10}(\text{C35}) + b_4 T + b_0$
2	$\log_{10}(\text{GR}) = b_1 \log_{10}(\text{SZB}) + b_2 \text{SD} + b_3 \log_{10}(\text{C35}) + b_4 T + b_0$
3	$\log_{10}(\text{GR}) = b_1 B_D + b_2 B_{Ca} + b_3 B_{Cy} + b_4 B_B + b_5 \text{SD} + b_6 \log_{10}(\text{C35}) + b_7 T + b_0$
4	$\log_{10}(\text{GR}) = b_1 B_{Cl} + b_2 B_{Co} + b_3 \text{SD} + b_4 \log_{10}(\text{C35}) + b_5 T + b_0$

TABLE 2. Site characteristics where zooplankton were sampled. All zooplankton was collected at night, except for Upton 5 which was sampled during the day. Most lakes were sampled in 1989 except for Popolopen 0, Stilwell, and Tyrrel 0 which were sampled in 1988. TEMP is water temperature at 1 m depth, TOTCHL is total chlorophyll concentration, C35 is the concentration of chlorophyll in algae <35 μm , ZB is zooplankton biomass, SZB is zooplankton biomass excluding adult and copepodite cyclopoids, and MEAN is mean zooplankton body weight. Dominant zooplankton taxa are listed in decreasing order of importance and collectively represent at least 90% of the biomass. *B* is *Bosmina longirostris*, *Ca* is calanoids, *Ce* is *Ceriodaphnia quadrangula*, *Cy* is cyclopoids, *D* is *Daphnia* spp., *Di* is *Diaphanosoma brachyurum*, and *H* is *Holopedium gibberum*. —, not measured.

Lake	County, State	Date (mo/d)	TEMP (°C)	TOTCHL ($\mu\text{g}\cdot\text{L}^{-1}$)	C35 ($\mu\text{g}\cdot\text{L}^{-1}$)	ZB ($\text{mg}\cdot\text{L}^{-1}$)	SZB ($\text{mg}\cdot\text{L}^{-1}$)	MEAN (μg)	Dominant taxa
Bull	Orange, NY	07/24	24.0	3.3	2.4	0.094	0.029	0.42	Cy, <i>B</i>
East Twin	Litchfield, CT	08/16	24.0	3.4	2.3	0.240	0.227	7.09	<i>D</i>
Gilead	Putnam, NY	08/08	23.5	4.9	3.9	0.189	0.103	1.04	Cy, <i>Ce</i> , <i>B</i> , <i>D</i>
Giles	Pike, PA	06/26	23.0	0.8	0.3	0.243	0.243	1.54	<i>D</i> , <i>Ca</i>
Gleneida	Putnam, NY	07/20	22.5	14.9	10.9	0.339	0.118	0.90	Cy, <i>B</i> , <i>Ce</i>
Lacawac	Wayne, PA	06/25	24.0	3.0	2.4	0.110	0.072	2.62	<i>D</i> , Cy, <i>Ca</i>
Lincoln	Albany, NY	08/19	20.0	4.7	3.6	0.359	0.072	1.17	Cy, <i>B</i>
Myosotis 1	Albany, NY	06/09	23.0	11.3	7.3	0.413	0.329	2.08	<i>D</i> , Cy, <i>B</i>
Myosotis 2	Albany, NY	07/11	22.0	16.4	9.2	0.527	0.410	2.63	<i>D</i> , Cy, <i>B</i>
Myosotis 3	Albany, NY	08/19	21.0	70.5	40.0	0.670	0.579	2.95	<i>Di</i> , <i>D</i> , Cy, <i>Ca</i>
Myosotis 4	Albany, NY	09/24	15.0	14.7	5.9	0.451	0.401	3.71	<i>D</i> , <i>Di</i> , Cy
Popolopen 0	Orange, NY	10/10	14.0	7.6	3.5	0.073	0.053	1.80	<i>D</i> , Cy, <i>Ca</i>
Popolopen 1	Orange, NY	05/22	20.5	3.4	1.6	0.048	0.037	1.12	<i>Ca</i> , Cy, <i>D</i>
Round	Orange, NY	05/24	21.0	—	6.0	0.413	0.376	1.10	<i>B</i> , <i>Ca</i> , Cy
Stilwell	Orange, NY	10/11	14.0	21.3	18.8	0.028	0.003	1.09	Cy, <i>B</i>
Tyrrel 0	Dutchess, NY	09/13	21.0	12.5	6.3	0.213	0.182	1.19	<i>Ce</i> , Cy, <i>D</i> , <i>Ca</i>
Tyrrel 1	Dutchess, NY	06/05	24.0	4.1	3.0	0.627	0.304	1.23	Cy, <i>Ca</i> , <i>Ce</i> , <i>D</i>
Tyrrel 2	Dutchess, NY	07/17	22.5	18.1	12.7	0.498	0.379	2.11	<i>D</i> , <i>Ca</i> , Cy
Tyrrel 3	Dutchess, NY	08/09	24.0	11.9	10.1	0.350	0.054	3.53	Cy, <i>Ca</i>
Tyrrel 4	Dutchess, NY	09/07	21.0	9.7	8.3	0.164	0.080	0.80	Cy, <i>Ca</i> , <i>D</i> , <i>N</i>
Tyrrel 5	Dutchess, NY	10/18	12.0	14.3	8.9	0.289	0.200	1.06	<i>Ca</i> , Cy, <i>B</i> , <i>Ce</i> , <i>N</i>
Upton 1	Dutchess, NY	04/26	13.5	—	3.5	0.917	0.803	2.84	<i>D</i> , Cy, <i>Ca</i>
Upton 2	Dutchess, NY	05/31	22.0	9.9	3.7	1.237	1.081	7.78	<i>D</i> , Cy, <i>Ca</i>
Upton 3	Dutchess, NY	07/05	24.5	5.7	2.2	0.468	0.371	7.90	<i>D</i> , Cy
Upton 4	Dutchess, NY	08/07	23.0	5.9	3.2	0.364	0.335	6.04	<i>D</i> , Cy
Upton 5	Dutchess, NY	09/11	22.0	4.2	2.2	0.043	0.030	1.94	<i>D</i> , Cy, <i>N</i>
Upton 6	Dutchess, NY	09/11	22.0	3.1	1.6	0.592	0.572	6.77	<i>D</i>
Waynewood	Wayne, PA	06/27	25.0	12.8	2.6	1.021	0.997	7.69	<i>D</i>
West Branch	Putnam, NY	08/14	22.5	9.0	4.0	0.174	0.080	1.46	Cy, <i>Ce</i> , <i>D</i> , <i>B</i> , <i>H</i>
Wononscopomuc	Litchfield, CT	08/16	24.0	2.1	1.5	0.102	0.077	1.92	<i>D</i> , Cy

commonly used methods based on the ingestion of specific types of labelled food particles (e.g. Haney 1973; Bogdan and Gilbert 1987), the method that we used measures grazing rates on a portion of the in situ algal community over a longer time period (1.5 d compared to 10–30 min).

Our measurements approximate zooplankton community ingestion rates. These estimates are based on the disappearance of chlorophyll, uncorrected for pheopigments, and would be in error if egestion of pigments confounded our measurement of disappearance. Ingested chlorophyll has four fates. Chlorophyll can be assimilated, converted to nonfluorescent pigments (Conover et al. 1986; Lopez et al. 1988), converted to fluorescent pheopigments (pheophytin and pheophorbide; Daley 1973), or egested unchanged. Our method would underestimate ingestion if the latter two pathways were large. Increases in pheopigments as a consequence of grazing would be detected as chlorophyll and would lead to underestimates of ingestion. Because we found no effect of pheopigments on calculations of grazing in selected manipulations (see Methods), we conclude that pheopigment production was not large. The passage of chlorophyll unaltered through the gut of grazers would also lead to underestimates of ingestion. Other studies, however, demonstrated that little chlorophyll passes unaltered through the gut; rather, on average, 92% is converted to pheopigments and nonfluorescent pigments ($n = 38$; Daley 1973; Dagg and Wal-

ser 1987; Head 1988; Lopez et al. 1988; Penry and Frost 1991). We conclude that in our study, these potential problems were not sufficient to cause large errors in our grazing estimates.

Zooplankton grazed per day 2–21% of the chlorophyll in algae <35 μm ($0.02\text{--}0.23\cdot\text{d}^{-1}$; Table 3). Standard errors were 10 to >100% of mean estimates, low precision being mostly associated with small grazing rates (SE exceeded 35% of the mean only for grazing rates smaller than $0.06\cdot\text{d}^{-1}$). Despite nutrient saturation, the realized growth of algae in the absence of macrozooplankton (*A*, the intercept of equation 1) varied widely among manipulations (Table 3). Such variation can result from differences in phytoplankton community structure, physiological status of algae in different communities, microzooplankton grazing, and light degradation of chlorophyll. Chlorophyll concentration decreased by as much as $49\%\cdot\text{d}^{-1}$ ($\ln(C_1/C_0) = -0.67$ in Tyrrel 3) or increased by $146\%\cdot\text{d}^{-1}$ ($\ln(C_1/C_0) = 0.90$ in Gilead) in different manipulations. Chlorophyll concentration mostly decreased in spring and fall manipulations. Differences in *A* reflect differences among communities but do not bias our grazing rate measurements.

Prediction of Community Grazing Rates

Grazing rates measured in different communities vary with zooplankton biomass, food concentration, and zooplankton taxonomic composition, but much variation remains unex-

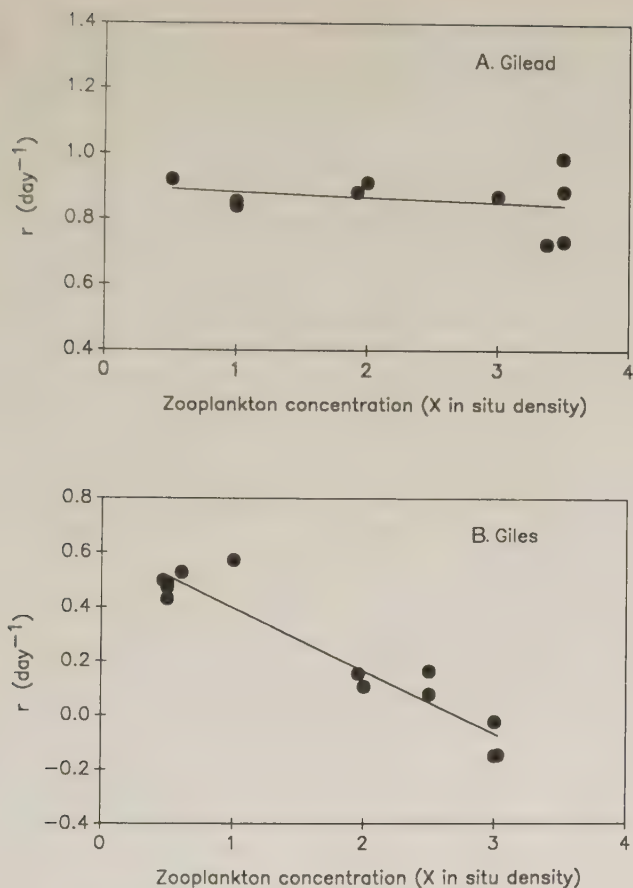


FIG. 1. Measurement of grazing rate in (A) Gilead ($r^2 = 0.06$) and (B) Giles ($r^2 = 0.91$). Each point represents an enclosure. As zooplankton concentration is increased, the realized growth rate of algae (r) decreases. Grazing rate is the absolute value of the slope of the relationship. The intercept is a measure of realized growth rate with excess nutrients in the absence of macrozooplankton.

plained. Three models explain 19–35% of the variability in grazing rate among zooplankton communities (Table 4A). Grazing rates were negatively related to food concentration and positively related to zooplankton biomass (models 2 and 3, Table 4A). Communities with high calanoid biomass tend to have high grazing rates (model 3, Table 4A), while cyclopoids appear, in general, to be unimportant herbivores (SZB, but not ZB, is related to grazing rate; compare models 2 and 1, Table 4A). Many of these coefficients, however, are marginally significant ($0.05 > P(t) > 0.01$), considering the large number of variables that were measured. We did not detect any effect of community size structure or water temperature on grazing rate ($P > 0.05$). Zooplankton community grazing rate was poorly related to variables that are usually considered most important.

Within lakes, seasonal changes in zooplankton grazing rates are usually attributed to differences in zooplankton biomass, food concentration, and water temperature (Gulati et al. 1982; Lampert and Taylor 1985; Hart 1986; Lampert 1988). As in our models, grazing rates increase with zooplankton biomass (Gulati et al. 1982; Lampert and Taylor 1985; Hart 1986; Lampert 1988) and decrease with increasing food concentration (Gulati et al. 1982; Hart 1986). Bleiwas and Stokes (1990) found grazing rates increasing with chlorophyll concentration, but their data were limited to oligotrophic lakes ($0.3\text{--}3\ \mu\text{g}$ chlorophyll $\cdot \text{L}^{-1}$), and they found no relationship between grazing rates and algal biovolumes. Variation in zooplankton grazing

TABLE 3. Zooplankton community grazing rate (GR) and realized algal growth rate in the absence of macrozooplankton (A) for each manipulation (standard errors in parentheses). They are, respectively, the slope (b) and the intercept (A) of equation 1. n is the number of enclosures used to determine grazing rate.

Lake	GR (d^{-1})	A (d^{-1})	n
Bull	0.02 (0.01)	0.23 (0.02)	10
East Twin	0.05 (0.02)	0.02 (0.07)	10
Gilead	0.02 (0.02)	0.90 (0.08)	10
Giles	0.23 (0.02)	0.63 (0.08)	13
Glencida	0.04 (0.01)	0.56 (0.05)	12
Lacawac	0.15 (0.02)	0.04 (0.12)	12
Lincoln	0.03 (0.03)	0.34 (0.06)	10
Myosotis 1	0.20 (0.04)	-0.03 (0.15)	14
Myosotis 2	0.04 (0.01)	-0.15 (0.05)	10
Myosotis 3	0.03 (0.03)	0.06 (0.03)	9
Myosotis 4	0.04 (0.01)	-0.17 (0.04)	12
Popolopen 0	0.09 (0.02)	-0.14 (0.08)	10
Popolopen 1	0.13 (0.02)	-0.26 (0.06)	8
Round	0.16 (0.04)	-0.34 (0.19)	12
Stilwell	0.04 (0.01)	-0.07 (0.07)	9
Tyrrel 0	0.05 (0.02)	-0.38 (0.10)	12
Tyrrel 1	0.17 (0.02)	0.12 (0.09)	14
Tyrrel 2	0.03 (0.02)	0.36 (0.06)	12
Tyrrel 3	0.03 (0.01)	-0.67 (0.03)	10
Tyrrel 4	0.03 (0.01)	-0.39 (0.01)	8
Tyrrel 5	0.08 (0.02)	0.01 (0.06)	12
Upton 1	0.13 (0.04)	0.27 (0.11)	15
Upton 2	0.06 (0.03)	-0.20 (0.10)	12
Upton 3	0.08 (0.02)	0.20 (0.09)	12
Upton 4	0.10 (0.02)	0.22 (0.04)	10
Upton 5	0.04 (0.03)	0.23 (0.17)	12
Upton 6	0.07 (0.02)	-0.01 (0.07)	12
Waynewood	0.19 (0.04)	0.19 (0.09)	14
West Branch	0.07 (0.03)	0.33 (0.04)	8
Wononscopomuc	0.04 (0.02)	0.14 (0.08)	12

TABLE 4. Models relating grazing rate (GR, d^{-1}) to characteristics of the zooplankton communities and of the environments (see models tested in Table 1). Communities of large zooplankton have at least 60% of their biomass as *Daphnia* and *Diaphanosoma*. R^2 are given for each equation. SMEAN is mean zooplankton body weight excluding adult and copepodite cyclopoids (μg) and ZM_b is the Elser et al. (1987) body size coefficient (μg). Other abbreviations and model numbers are as in Table 1.

Model	Equation	R^2
(A) All communities ($n = 30$)		
1, 4	$\log(\text{GR}) = -0.3 \log(\text{C35}) - 1.0$	0.19
2	$\log(\text{GR}) = 0.2 \log(\text{SZB}) - 0.3 \log(\text{C35}) - 0.8$	0.30
3	$\log(\text{GR}) = 2.8 B_{\text{Ca}} - 0.4 \log(\text{C35}) - 1.1$	0.35
(B) Small zooplankton ($n = 18$)		
1, 3	$\log(\text{GR}) = -0.4 \log(\text{C35}) - 0.9$	0.23
2	$\log(\text{GR}) = 0.7 \log(\text{SMEAN}) - 1.1$	0.33
4	$\log(\text{GR}) = 1.6 B_{\text{Cl}} - 0.5 \log(\text{C35}) - 1.0$	0.41
(C) Large zooplankton ($n = 12$)		
1a	$\log(\text{GR}) = 0.4 \log(\text{ZB}) - 0.4 \log(\text{C35}) - 0.8$	0.60
1b	$\log(\text{GR}) = 1.2 \log(\text{ZM}_b) - 2.2$	0.61

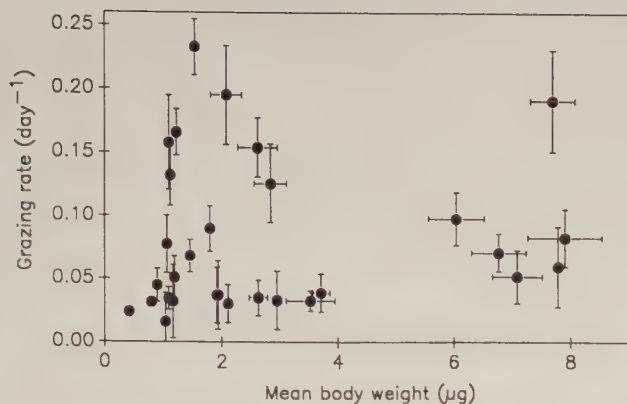


FIG. 2. Community grazing rate in zooplankton communities of different mean body weight. Standard errors are shown for both variables, but in some cases are smaller than the symbol for the data point.

rates appears to be related to zooplankton biomass and to food concentration, both seasonally within a lake and among lakes.

Water temperature affects zooplankton grazing rates in temperate lakes (Haney 1973; Gulati et al. 1982). Temperature is positively related to community grazing rates measured year-round, but its effect is less clear from April to October, when temperatures rise above 10°C. Similarly, temperature effects often cannot be detected for individual taxa of cladocerans and copepods (Zankai 1978; Peters and Downing 1984; Chow-Fraser and Knoechel 1985; Chow-Fraser 1986; Knoechel and Holtby 1986; Bleiwas and Stokes 1990; but see Mourelatos and Lacroix 1990). Concurrent changes in biomass and taxonomic composition of zooplankton and phytoplankton probably overshadow the effect of temperature on physiological rates. Water temperature was not related to zooplankton community grazing rates during the summer months.

Residual variation in grazing rates has been attributed to zooplankton size and taxonomic composition (Gulati et al. 1982; Hart 1986). In the communities we studied, the parameters of zooplankton size distributions (arithmetic mean, median and Elser coefficient of mean body size, variance and skewness of size distributions), and the slope of normalized size distributions were not related to grazing rate. Taxonomic composition had a statistically significant effect on grazing rate, although it explained very little of the variation among communities (Table 4A).

Cyclopoids were not important herbivores in the lakes we sampled. It is interesting to note that grazing rate was related to zooplankton biomass when excluding adult and copepodite cyclopoids but not to total zooplankton biomass (models 2 and 1, Table 4A). These results suggest that cyclopoids may, in many communities, not be important grazers of algae <35 μm. The abundance of cyclopoids in a community probably has to be taken into account in order to predict grazing rate from zooplankton biomass.

Calanoids can be important grazers. Community grazing rates increased with calanoid biomass (model 3, Table 4A). Calanoid biomass is not simply a surrogate for total biomass in this relationship because the two variables are poorly correlated (B_{Ca} versus STB: $r^2 = 0.22$) compared with *Daphnia* and cladoceran biomass (B_D versus STB: $r^2 = 0.50$; B_{Cl} versus STB: $r^2 = 0.61$). Previous studies have found that calanoids graze less than cladocerans of similar sizes (Peters and Downing 1984; Knoechel and Holtby 1986). We therefore expected calanoids to contribute little to community grazing. Some of the highest grazing rates we measured, however, were from communities

with large proportions of calanoids (e.g. Giles with 46% calanoid and 51% *Daphnia* biomass; Round with 38% calanoid, 43% *Bosmina*, and 15% cyclopoids; Popolopen 1 with 61% calanoid, 22% cyclopoid, and 8% *Daphnia* biomass). Calanoid grazing rates vary with food particle size and shape (Vanderploeg 1981; Chow-Fraser 1986; Vanderploeg et al. 1988), and their grazing may have been underestimated from studies based on one or a few food particle sizes. We found that in mixed communities, grazing rates tend to increase with calanoid biomass.

Grazing rate was significantly but weakly related to zooplankton biomass and taxonomic composition and to food concentration. Much variation, however, remains unexplained. It has been suggested that because different algal species are grazed at different rates, algal composition should be important in determining total zooplankton grazing rate (Lehman and Sandgren 1985; Vanni and Temte 1990). Many aspects of algal size, shape, surface properties, and chemical composition have been shown to affect zooplankton grazing rates (Peters 1984; Sterner 1989; Vanderploeg 1990), but the importance of these parameters in natural communities is still unclear. The characteristics of phytoplankton assemblages that are most strongly related to zooplankton grazing rates in natural communities remain to be determined and their effect needs to be quantified.

Zooplankton Size Structure and Herbivory

Surprisingly, in the lakes we sampled, communities dominated by *Daphnia* (mean size of zooplankton >5 μg) did not graze at higher rates than communities of smaller zooplankton (Fig. 2). We expected communities of large zooplankton to graze more than communities of small zooplankton for four reasons. (1) Large zooplankton can exploit a wider range of food particle sizes (Burns 1968; Gliwicz 1977). (2) Very high grazing rates associated with the period of phytoplankton disappearance found in spring in some lakes (clear water phase) are attributed to large biomasses of *Daphnia* (Lampert et al. 1986), not of smaller zooplankton. (3) Biomanipulation and cascading trophic interaction hypotheses predict that an increase in the biomass of large zooplankton, from reduced planktivory, should result in lower phytoplankton biomass (Shapiro 1980; Carpenter et al. 1985). These predictions appear to be most successful in communities dominated by large *Daphnia* (Shapiro and Wright 1984; Carpenter et al. 1987). (4) The ratio of chlorophyll to phosphorus concentration tends to be lower in lakes with large zooplankton (Hrbáček et al. 1978; Pace 1984), especially when large (>1 mm) cladocerans are present (Pace 1984). Our data, however, suggest that total zooplankton biomass, not size structure, is related to community grazing rate of algae <35 μm (Table 4A). There are three possible explanations that could reconcile our observations to the results of other authors. First, the effect of size structure on community grazing rates may only be expressed with larger cladocerans. The largest cladocerans that we sampled had an average length of 1.2 mm. We cannot rule out the possibility that had we considered communities with even larger cladocerans, we would have found an effect of community size distribution on grazing rate. The second possible explanation is that differences in size-selective grazing between small and large zooplankton are strongest for algae >35 μm. Burns (1968) and Gliwicz (1977), however, found differences with particles <35 μm in diameter. Both studies were based on the ingestion of artificial particles; the hypothesis remains to be tested with algal cells. A third explanation could be that large crustaceans had modified the phytoplankton assemblage avail-

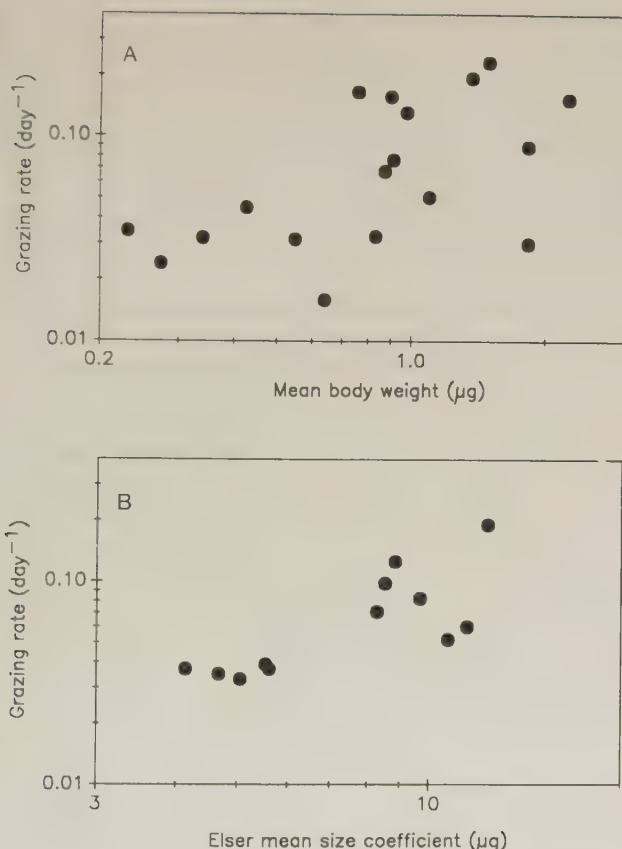


FIG. 3. (A) Relationship between grazing rates and mean weight of zooplankton, excluding nonnaupliar cyclopoids, in communities dominated by small crustaceans ($n = 18$; $r^2 = 0.33$). (B) Relationship between grazing rates and the Elser et al. (1987) coefficient of mean size in communities dominated by *Daphnia* and *Diaphanosoma* ($n = 12$; $r^2 = 0.61$).

able for grazing (Vanni and Temte 1990). According to this scenario, an initial period of high grazing rates when large crustaceans first establish would be followed by lower grazing rates, and communities of large zooplankton should typically be associated with communities of relatively inedible phytoplankton. We observed differences in the composition of algal communities which are consistent with this hypothesis. The proportion of "edible" algae (i.e. chlorophyll in algae $< 35 \mu\text{m}$) was lower in communities dominated by *Daphnia* and *Diaphanosoma* (range 20–71%, median = 53%) compared with communities dominated by small crustaceans (range 38–100%, median = 72%). These observations do not reject the third possible explanation, but it is not clear that they can account for the grazing rates we measured. In the range of communities we sampled, we could not detect a relationship between community size distribution and zooplankton grazing rate on algae $< 35 \mu\text{m}$.

Community size structure was related to zooplankton grazing rate in subsets of the communities we sampled. In communities dominated by small zooplankton, where the biomass of *Daphnia* and *Diaphanosoma* represents less than 60% of zooplankton biomass, grazing rates increased with the mean size of noncyclopoid crustaceans (Fig. 3A; model 2, Table 4B). Mean size was not a surrogate for biomass in this equation, as the same relationship was obtained when biomass was decomposed into its constituents ($\log(\text{mean size}) + \log(\text{density})$). In communities dominated by *Daphnia* and *Diaphanosoma* ($> 60\%$ of zooplankton biomass), grazing rates increased with

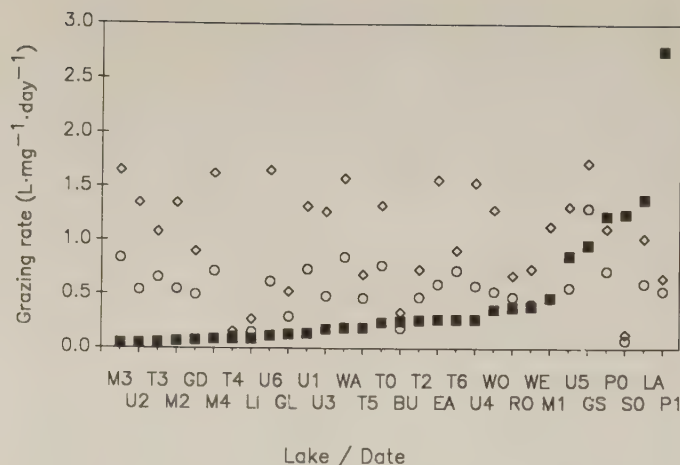


FIG. 4. Comparison of measured grazing rates (closed symbols) and grazing rates predicted from allometric equations (Chow-Fraser and Knoechel 1985: open circles, Knoechel and Holtby 1986: open diamonds) in 30 zooplankton communities. Predictions from the third model (Peters and Downing 1984) tend to fall between the predictions from the other two models. Zooplankton communities are from the following: BU, Bull; EA, East Twin; GD, Gilead; GL, Gleneida; GS, Giles; LA, Lacawac; LI, Lincoln; M1–4, Myosotis; P0–1, Popolopen; RO, Round; SO, Stilwell; T0–5, Tyrrel; U0–6, Upton; WA, Wayne-wood; WE, West Branch; WO, Wononscopomuc.

the Elser et al. (1987) coefficient of mean size (Fig. 3B; model 1b, Table 4C). We expected the opposite relationship between grazing rate and zooplankton size structure, especially in communities not dominated by *Daphnia*, because for a given biomass, large organisms usually have lower metabolic rates than small organisms (Peters 1983; Peters and Downing 1984). Positive relationships, as we found, could possibly result from larger organisms utilizing a wider range of food sizes (Burns 1968; Wilson 1973; Gliwicz 1977; Bogdan and Gilbert 1984). It is not clear, however, why the positive relationship between zooplankton mean body size and grazing rates is not continuous over all communities.

Different models were found to explain the variability in grazing rates of communities dominated by small or by large zooplankton. Around 40% of the variation in grazing rates among communities of small zooplankton was explained by cladoceran biomass and food concentration (model 4, Table 4B). The grazing rate of communities dominated by *Daphnia* and *Diaphanosoma* was equally well related ($R^2 = 0.60$, Table 4C) to zooplankton biomass and food concentration and to the Elser et al. (1987) coefficient of mean body size (models 1a and 1b, Table 4C). We can, therefore, explain, at most, 60% of the variation in grazing rates among zooplankton communities. This would lead to large errors around predictions we would make. For example, using our best model at its centroid (model 1b, Table 4C, $\log(ZM_B) = 0.87$), SE is 14% of individual prediction. Other models that include communities dominated by small zooplankton would lead to larger errors. Zooplankton grazing rates cannot be predicted with good precision using simple variables.

Predictions Using Allometric Equations

Allometric relationships provided biased estimations of grazing rates on algae $< 35 \mu\text{m}$ (Fig. 4). The equation of Chow-Fraser and Knoechel (1985) generally gave the best predictions, although in 30% of the communities, grazing rate was overestimated by at least four times, and in two communities the

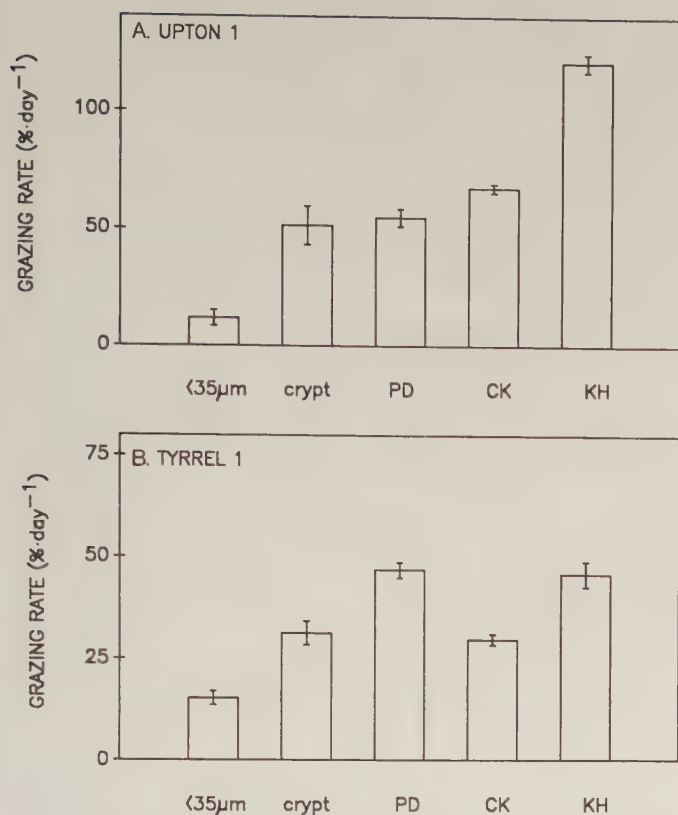


FIG. 5. Comparison of grazing rates measured on algae $<35\ \mu\text{m}$ and cryptomonads (crypt) and predicted using the equations of Peters and Downing (PD), Chow-Fraser and Knoechel (CK), and Knoechel and Holtby (KH) for (A) Upton 1 and (B) Tyrrel 1. Standard errors are shown.

predictions were less than 20% of the measured rates. Using the equations of Peters and Downing (1984) and of Knoechel and Holtby (1986), more than 40% of the predictions overestimated grazing rates by fourfold or more. Different models varied widely in their ability to predict grazing rate.

The discrepancy between predicted and measured grazing rates could result from the different foods that are considered. Allometric equations predict grazing rates on one, usually highly edible food particle. The method that we used measures grazing rate on an entire fraction of the algal community (cells $<35\ \mu\text{m}$) that probably includes highly edible and less edible algae. We found, indeed, that grazing rates measured on cryptomonads only were much higher (two- and fourfold) than those measured on all algae $<35\ \mu\text{m}$ and were closer to rates predicted using allometric equations (Fig. 5). Allometric equations gave good estimations of grazing rate on cryptomonads but overestimated grazing on algal mixtures. These comparisons suggest that a substantial proportion of the chlorophyll in algae $<35\ \mu\text{m}$ was not readily edible.

Magnitude of Zooplankton Grazing Rates

Zooplankton grazed, on average, less than $8\% \cdot \text{d}^{-1}$ of the chlorophyll in algae $<35\ \mu\text{m}$ (Table 3). Our measurements fall in the same range as more than half of the observations that we compiled from the literature (Fig. 6). Zooplankton grazing rates can be very high, e.g. 464 and $317\% \cdot \text{d}^{-1}$ measured by Haney (1973) and above $200\% \cdot \text{d}^{-1}$ measured by Gliwicz and Hillbricht-Ilkowska (1972), Jarvis (1986), and Mazumder et al. (1990), but most (75%) grazing rate measurements are below $50\% \cdot \text{d}^{-1}$ (Fig. 6).

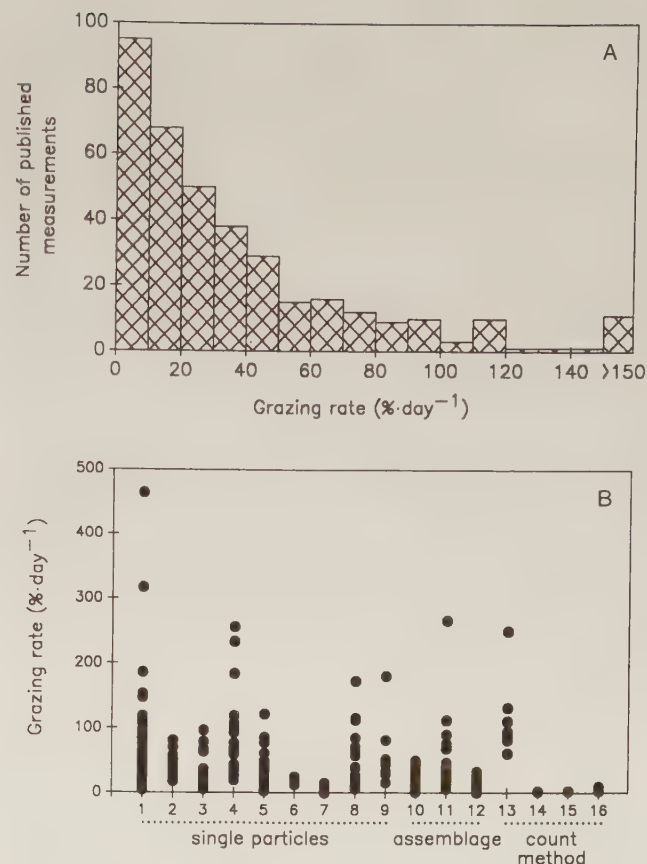


FIG. 6. (A) Frequency distribution of zooplankton grazing rate measurements compiled from the literature ($n = 369$). We included grazing rates measured in the epilimnion, during the main growing season (April to October in lakes of the Northern Hemisphere, October to April in New Zealand, and all years in South African lakes). 51% of the observations were less than $25\% \cdot \text{d}^{-1}$. (B) Distribution of grazing rates measured by different authors. Grazing rates were measured on single radioactively labelled food particles (1, Haney 1973; 2, Sierszen and Frost 1990; 3, Bleiwas and Stokes 1990; 4, Jarvis 1986; 5, Thompson et al. 1982; 6, James and Forsyth 1990; 7, Hart 1986; 8, Lampert and Taylor 1985 and Lampert et al. 1986; 9, Gawler and Angeli 1987), on radioactively labelled algal assemblages (10, Gulati 1975 and Gulati et al. 1982; 11, Mazumder et al. 1990; 12, Zankai and Panyi 1986), and with modifications of the algal count method (13, Gliwicz and Hillbricht-Ilkowska 1972; 14, Bergquist and Carpenter 1986; 15, Dorazio et al. 1987; 16, Scavia and Fahnenstiel 1987).

The magnitude of phytoplankton removal by zooplankton may have been overestimated by many previous measurements of grazing rates. A large number of the grazing rates we gathered from the literature (61%) were measured on single, usually highly edible food particles (e.g. *Chlamydomonas*, *Chlorella*, *Rhodomonas*; Fig. 6B). These rates may be good estimates of total removal of algae when all algae are grazed equally. Algal communities, however, are almost always diverse. Because grazing varies with the size, shape, and taste of the algae (Gliwicz 1969; Peters and Downing 1984; DeMott 1986; Bogan and Gilbert 1987), grazing rates measured on one alga cannot be extrapolated easily to whole algal communities (Gliwicz 1969; Lampert 1988). We found the grazing of cryptomonads to be two and four times faster than grazing of algae $<35\ \mu\text{m}$ in Tyrrel 1 and Upton 1, respectively (Fig. 5). Similarly, James and Forsyth (1990) found grazing rates measured with radioactively labelled *Cyclotella* to be five times higher than when measured by changes in chlorophyll content of the phytoplankton community.

Extrapolation of grazing rates measured on one food particle to an algal community requires that we integrate the relationship between grazing rate and food particle characteristics (e.g. particle size: Gliwicz 1969; Vanderploeg 1981; McCauley and Downing 1985) and the characteristics of food particles found in situ (e.g. frequency distribution of particle size). Models relating grazing rate to food particle characteristics, however, are still preliminary (McCauley and Downing 1985; Peters and Downing 1984), and data on in situ food particle distribution are difficult to obtain. Further consideration of the composition of phytoplankton assemblages (e.g. size, morphology, and chemical composition) may be required to improve our predictions of herbivory in freshwater pelagic systems.

Crustaceans can have a dramatic impact on phytoplankton (e.g. Shapiro and Wright 1984; Edmondson and Litt 1982; Carpenter et al. 1987; Lampert et al. 1986) but usually only graze a small proportion of the algal biomass per day. These results suggest that changes in herbivory resulting from the manipulation of higher trophic levels may not be solely responsible for the observed response of phytoplankton. Other changes associated with the size structure of crustacean communities, e.g. in rates of nutrient cycling (Sterner 1989; Vanni and Findlay 1990), may also be important in determining phytoplankton response.

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Planktivores and Plankton Dynamics: Effects of Fish Biomass and Planktivore Type

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We quantified the effects of planktivore biomass and planktivore type in an experimental mesocosm study of factorial design in which five levels of fish biomass (0–75 g/m³) were cross-classified with two planktivore types: filter-feeding gizzard shad (*Dorosoma cepedianum*) and visual-feeding bluegill (*Lepomis macrochirus*). As fish biomass increased, cladocerans, cyclopoids, particulate phosphorus (PP) >200 µm, and chironomids declined; conversely, rotifers, primary productivity, chlorophyll *a*, turbidity, unicellular flagellates, colonial and unicellular green algae, pennate diatoms, total phosphorus, and 20–200 and 12–20 µm PP were enhanced. In the presence of gizzard shad, as compared with bluegill, cyclopoids, turbidity, unicellular green algae, pennate diatoms, >200 µm PP, and chironomid tubes were higher whereas colonial green algae and <0.2 µm PP were lower. Fish biomass operated independently of planktivore type for most variables, except copepods, colonial green algae, turbidity, and 20–200 µm PP. Although gizzard shad and bluegill have different trophic cascade pathways, fish biomass was more important than planktivore type as a regulator of plankton communities and water quality.

Les auteurs ont quantifié les incidences de la biomasse et du type de planctophage dans le cadre d'une étude expérimentale en mésocosmes. Cette étude était conçue en fonction d'un plan factoriel d'expérience combinant cinq niveaux de biomasse de poisson (de 0 à 75 g/m³) avec deux types de planctophage, soit l'aloise à gésier (*Dorosoma cepedianum*), un filtreur, et le crapet arlequin (*Lepomis macrochirus*), un chasseur visuel. Une augmentation de la biomasse de poisson était accompagnée d'une baisse du nombre de cladocères, de cyclopoïdes et de chironomides et de la teneur en phosphore particulaire (PP) >200 µm; inversement, l'abondance de rotifères, de flagellés unicellulaires, d'algues vertes coloniales et unicellulaires, de diatomées pennées, la productivité primaire, la turbidité et les teneurs en chlorophylle *a*, en phosphore total et en PP de 20 à 200 µm et de 12 à 20 µm ont augmenté. En présence de l'aloise à gésier, l'abondance de diatomées pennées, de cyclopoïdes, d'algues vertes unicellulaires et de tubes de chironomides, la turbidité et la teneur en PP >200 µm étaient plus élevées que lorsque le crapet arlequin était présent; par contre, l'abondance d'algues vertes coloniales et la teneur en PP <0,2 µm étaient moins élevées. L'influence de la biomasse de poisson était indépendante du type de planctophage pour la plupart des variables, sauf en ce qui concerne les copépodes, les algues vertes coloniales, la turbidité et le PP de 20 à 200 µm. Bien que la chaîne des cascades trophiques de l'aloise à gésier et celle du crapet soleil soient différentes, la biomasse de poisson jouait un rôle plus important que le type de planctophage comme régulateur des communautés planctoniques et de la qualité de l'eau.

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Planktivorous fish regulate phytoplankton and water quality of lakes through their consumption of plankton and alteration of nutrient cycles (Lazzaro 1987; Vanni 1987a; Northcote 1988). How planktivorous fish influence plankton

and water quality depends on fish biomass (McQueen et al. 1986; Threlkeld 1988; Drenner and Smith 1991). Empirically derived regressions demonstrate negative relationships between planktivore biomass and zooplankton biomass as well as between zooplankton biomass and phytoplankton biomass (Vijverberg and van Densen 1984; McQueen and Post 1985; McQueen et al. 1986). These functional relationships between planktivore biomass and plankton biomass appear to be nonlin-

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ear (Drenner et al. 1987; Threlkeld 1988; Drenner and Smith 1991).

Although differences in the biomass-related effects of the two types of planktivores, filter feeders and visual feeders, on plankton and water quality are unknown, studies (Drenner et al. 1986; Lazzaro 1987) suggest that these two planktivore types have different trophic cascade pathways. Visual feeders locate and attack single zooplankton prey (Janssen 1976) whereas filter feeders do not visually detect individual prey, but strain prey and particles from engulfed water using gill rakers or other entrapment structures (Mummert and Drenner 1986; Drenner et al. 1987). Visual feeders directly suppress populations of large zooplankters, and may indirectly enhance populations of phytoplankton and small and or highly evasive zooplankton (Hambright et al. 1986). In contrast, pump filter feeders directly suppress populations of cladocerans and large phytoplankton, and indirectly enhance copepods and small algae (Kajak et al. 1977; Drenner et al. 1986, 1987).

To quantify how fish biomass and planktivore type affect plankton dynamics and water quality, and to determine whether the effects of fish biomass and planktivore type operate independently, we performed an experiment of factorial design in which five levels of fish biomass were cross-classified with two planktivore types. We used filter-feeding gizzard shad (*Dorosoma cepedianum*) and visual-feeding bluegill (*Lepomis macrochirus*), either of which can dominate the fish biomass of lakes and reservoirs in the central and southeastern United States (Jenkins 1967; Cooper et al. 1971). Gizzard shad (>40 mm standard length (SL)) an omnivorous pump filter-feeding clupeid, feeds on phytoplankton, zooplankton, and detritus (Mummert and Drenner 1986) whereas bluegill, a carnivorous centrarchid, feeds primarily on zooplankton and benthos (Werner 1977).

Material and Methods

We conducted this experiment in 20 white fiberglass tanks at the outdoor mesocosm facility at Texas Christian University. Tanks were 1.8 m in diameter, 2.2 m high, and contained about 5500 L. Tanks were continuously mixed with an airlift mixer system to prevent stratification (Drenner et al. 1986).

Because we were searching for generality and used the tanks as model systems, we did not try to synchronize conditions in tanks with those from any one lake or reservoir. We filled the tanks with water from a small (0.7 ha), shallow pond (2.5 m maximum depth) with bluegill and western mosquitofish (*Gambusia affinis*), but no piscivores. The zooplankton of the pond was dominated by small cyclopoid copepods and rotifers, with few cladocerans (R. W. Drenner, pers. obs.). Water was pumped into the tanks on 6 April 1989 using a gasoline-powered diaphragm pump. To stimulate the development of cladoceran populations, we added about 800 cladocerans (*Simocephalus* and *Daphnia*, mainly *D. pulex*) to each tank. These cladocerans were obtained from two holding tanks filled 1 mo before the experiment. Because sand is used by gizzard shad to break algal cells during digestion (R. W. Drenner, pers. obs.), 3.8 L of autoclaved brick sand was added to each tank on 10–11 April.

Beginning 16 April, 518 $\mu\text{g N/L}$ as NH_4Cl and 32 $\mu\text{g P/L}$ as H_3PO_4 (concentrations after adding to tanks) were added to each tank every other day. Based on previous experience (Drenner et al. 1989), adding N and P at these concentrations would help maintain a total nitrogen to total phosphorus (TN:TP) ratio similar to that of the source pond.

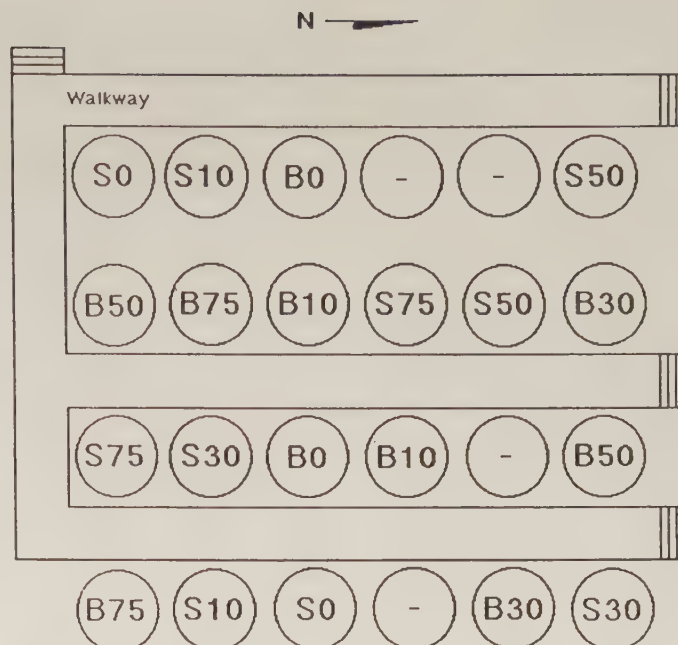


FIG. 1. Layout of the experimental tanks and sampling walkway. Assigned treatment combinations are indicated by the letters S (gizzard shad) and B (bluegill) for planktivore type followed by numbers indicating stocked fish biomass (0, 10, 30, 50, and 75 g/m^3 , wet mass).

On 7 April, bluegill and gizzard shad were electrofished from the pond and Interlocken Lake, Arlington, Texas, respectively, transported, and acclimated in holding tanks. On 15 April, fish were netted from these holding tanks, weighed in plastic bags (nearest 0.1 g), and stocked into experimental tanks according to the following design. Five levels of fish biomass (0, 10, 30, 50, and 75 g/m^3 , wet mass) were cross-classified with two levels of planktivore type (gizzard shad and bluegill) resulting in 10 treatment combinations. Each treatment combination was randomly assigned to tanks and replicated twice (Fig. 1). The two replicates of the no-fish treatment combination for gizzard shad (S0) were distinct from those for bluegill (B0). The five biomass levels were composed of 0, 1, 3, 5, and 7 gizzard shad and 0, 3, 9, 15, and 21 bluegill per tank. Mean individual weights (± 1 SD) and length ranges of stocked gizzard shad and bluegill were 53.8 ± 10.1 g (130–160 mm SL) and 17.2 ± 9.5 g (50–100 mm SL), respectively. Mean standing crops of gizzard shad (>200 kg/ha) (Schoonover and Thompson 1954; Aggus et al. 1979; Drenner et al. 1982; Hill 1983; Ali and Bayne 1987; Kirk and Davies 1987) are typically higher than those of bluegill (<200 kg/ha) (Carlander 1977; Aggus et al. 1979; Hill 1983; Hambright et al. 1986; Kirk and Davies 1987). We selected the maximum stocking biomass of 75 g/m^3 (about 1570 kg/ha) to ensure that gizzard shad were stocked across biomass gradients found in natural lake and reservoirs. Maximum gizzard shad biomass can be as high as 1236 kg/ha (Schoonover and Thompson 1954). To complete the factorial design, bluegill were stocked at similar biomass levels as gizzard shad even though maximum biomass reported for bluegill is 750 kg/ha (Carlander 1977). Therefore, biomass levels of 50 and 75 g/m^3 (about 1000 and 1500 kg/ha, respectively) were unrealistically high for bluegill.

Beginning 13 April (day 0), tanks were sampled at weekly intervals for 4 wk. Temperature was measured daily with a YSI model 43TD tele-thermometer and ranged from 12 to 25°C. Zooplankton were sampled with vertical tows of a 63- μm -mesh, 12-cm-diameter Wisconsin plankton net. Triplicate tows were

taken from each tank on each date, combined, preserved in 5% sucrose-formalin, and counted under a dissecting microscope. Densities were not corrected for net efficiency.

Integrated water column samples for analysis of turbidity, chlorophyll *a*, phytoplankton, total nitrogen (TN), total phosphorus (TP), and size fractions of particulate phosphorus (PP) were collected with a PVC tube lowered to near the tank bottom and then closed with a valve on the lower end of the tube. Turbidity was measured weekly with a Hach turbidimeter. Chlorophyll *a* samples on all dates were filtered through Millipore HAWP membrane filters (0.45- μm pore size), wrapped in aluminum foil, and frozen. Chlorophyll *a* was extracted in a 2:1 chloroform-methanol solution in the dark at 20–22°C for at least 4 h and absorbance measured at 665 nm (Wood 1985). Phytoplankton samples were preserved with 1.0% Lugol's iodine and settled overnight in sedimentation chambers. Seven to 10 random fields were counted (algae identified to genus) with an inverted microscope at 200 $\times$; algal densities were computed per taxonomic group. Phytoplankton sizes were determined by measuring 10 individuals per taxon using an ocular micrometer. Particles <2 μm were not counted.

Samples for TN were digested with alkaline potassium persulfate (D'Elia et al. 1977) and absorbance was measured at 220 nm (APHA 1985). Samples for TP were digested with potassium persulfate (Menzel and Corwin 1965) and analyzed using a modification of the malachite green method (Van Veldhoven and Mannaerts 1987) in which 1 mL of color reagent was added to 5-mL subsamples of the 20-mL total digestions and absorbance measured at 610 nm.

On days 0, 14, and 28, PP concentrations were determined for five size fractions: >200 μm (macroplankton), 20–200 μm (microplankton), 12–20 μm (large nanoplankton), 3–12 μm (small nanoplankton), and 0.2–3 μm (picoplankton) (Mazumder et al. 1988). Samples were fractionated within 1 h of collection with 47-mm Nuclepore polycarbonate filters with pore sizes of 0.2, 3, and 12 μm (50, 100, and 300 mL filtered, respectively) and prewashed 47-mm Nitex screens with mesh sizes of 20 and 200 μm (3 L filtered). After filtration (vacuum pressure <50 mm Hg, 1 mm Hg = 133.322 Pa), each filter was placed into a screw-capped test tube containing 35 mL of distilled and deionized water. Phosphorus concentrations in the fractionated samples were determined after oxidation with potassium persulfate with the same methodology used for TP. Filtrates (35 mL) passing through filters with a pore size of 0.2 μm were stored at 4°C and analyzed without the oxidation step. Because filtrates through 0.2- μm filters may actually contain viruses and ultramicrobacteria (0.02–0.2 μm), as well as phototrophic pico- and nanoplankton (0.2–2.0 μm), the phosphorus size fraction <0.2 μm may contain not only orthophosphate ($\text{PO}_4\text{-P}$) but some PP also (Stockner et al. 1990).

On days 1, 15, and 29, phytoplankton primary productivity was determined by in situ carbon fixation (^{14}C method) with two 250-mL light bottles and one 250-mL dark bottle (to correct for bacterial photosynthesis; Parkin and Brock 1980) incubated at 1 m in each tank from about 11:00 to 15:00. For each tank, an integrated water column sample collected with the PVC tube sampler was mixed in a pitcher and poured into the incubation bottles and then injected with 1 mL of a 3 $\mu\text{Ci/mL}$ (111 kBq/mL) solution of $\text{NaH}^{14}\text{CO}_3$. Initial dissolved inorganic carbon was calculated from total inflection point alkalinity (Gran 1952; Wetzel and Likens 1979). Immediately after incubations, 50 mL of each sample (stored in the dark) was filtered, collected on a Millipore HAWP membrane filter (0.45- μm pore size), exposed to 1 N HCl vapors for 30 min, dried

overnight, placed in a dioxane-base fluor, and counted with an automatic liquid scintillation counter.

On 16 and 17 May (days 33 and 34), tanks were drained through a fiberglass screen and fish removed, measured (SL, nearest 1 mm), and weighed (nearest 0.1 g). No fish died during the experiment. Immediately after tank draining, tube-dwelling chironomids and periphyton were sampled. Chironomid tubes were counted within a 1100-cm² rectangular area from the surface to a depth of 30 cm on one side of each tank. One 4 $\times$ 4 cm area of periphyton was removed with a razor blade from the center of the chironomid sampling area. Periphyton samples were collected on Millipore HAWP membrane filters (0.45- μm pore size), wrapped in aluminum foil, and frozen. Periphytic chlorophyll *a* was extracted by the method used for phytoplankton.

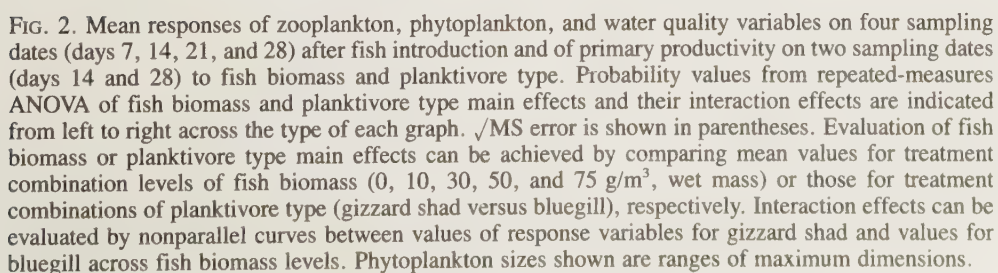
All statistical analyses were performed on SYSTAT (Wilkinson 1989). Because fish were stocked on day 2, data from day 0 were excluded from the analysis. Main effects of fish biomass and planktivore type and their interaction effects (fish biomass $\times$ planktivore type) were analyzed with repeated-measures ANOVA, using the Multivariate General Model Hypothesis with grouping factors (five fish biomasses and two planktivore types) and a time trial factor (two sampling dates, days 14 and 28, for primary productivity and PP and four sampling dates, days 7, 14, 21, and 28, for all other variables). Stocked fish biomass, fish growth rate (expressed in wet mass per stocked wet mass per day), periphytic chlorophyll *a*, and chironomid tube density were analyzed using a two-way ANOVA. Because of low replication and statistical power, we chose a probability level of $\alpha < 0.10$ to reduce the chance of making the type II error of failing to reject a false null hypothesis.

Results and Discussion

Fish biomass significantly affected densities of cladocerans (primarily *Daphnia pulex* and *Chydorus* sp.), cyclopoid copepods (primarily *Mesocyclops* sp. and *Acanthocyclops* sp., copepodids, and nauplii), and rotifers (primarily *Brachionus* sp. and *Asplanchna* sp.). With increasing fish biomass, densities of cladocerans and cyclopoid copepods decreased whereas densities of rotifers were enhanced (Fig. 2). Planktivore type affected cyclopoid densities, which were higher with gizzard shad than with bluegill. The difference in the effects of gizzard shad and bluegill may have occurred because filter-feeding gizzard shad capture cyclopoid copepods with less success than visual-feeding planktivores (Drenner and McComas 1980). However, day-0 cyclopoid densities were higher in tanks that were stocked with gizzard shad than in those that were stocked with bluegill (two-way ANOVA, $P = 0.017$), complicating our ability to interpret this planktivore type effect.

Fish biomass significantly affected primary productivity, phytoplankton chlorophyll *a*, turbidity, and densities of unicellular flagellates, colonial green algae, unicellular green algae, and pennate diatoms. All these variables increased with increasing fish biomass, except colonial green algae whose density declined at gizzard biomass >30 g/m³ (Fig. 2), possibly as a direct consequence of gizzard shad grazing. Planktivore type affected turbidity, unicellular green algae, colonial green algae, and pennate diatoms. All these response variables were higher in the presence of gizzard shad than with bluegill with the exception of colonial green algae.

For most plankton and water quality response variables, fish biomass and planktivore type acted independently, as revealed



by nonsignificant interaction terms ($P > 0.10$). We found significant fish biomass $\times$ planktivore type interactions only for cyclopoid copepods, turbidity, and colonial green algae. To examine these relationships, we computed simple effects to detect differences between gizzard shad and bluegill treatments at each biomass level. At 10 g/m^3 , cyclopoid densities were higher with gizzard shad than with bluegill ($P = 0.003$; Fig. 2). Turbidity was higher with gizzard shad than with bluegill at biomass $\geq 30 \text{ g/m}^3$ ($P < 0.01$). At 75 g/m^3 , densities of colonial green algae (primarily *Actinastrum* spp.) were higher with bluegill than with gizzard shad ($P = 0.001$). At this biomass, bluegill may have indirectly enhanced colonial green algae by suppressing *Daphnia* because small colonial green algae are particularly vulnerable to grazing by *Daphnia* (Vanni and Temte 1990) whereas gizzard shad may have directly reduced larger colonial green algae by grazing.

Fish biomass effects on PP were consistent with its effects on zooplankton and phytoplankton. Fish biomass reduced $>200 \text{ }\mu\text{m}$ PP (macroplankton) and enhanced $20\text{--}200 \text{ }\mu\text{m}$ PP (microplankton) and $12\text{--}20 \text{ }\mu\text{m}$ PP (large nanoplankton) (Fig. 3). Bluegill reduced $>200 \text{ }\mu\text{m}$ PP more dramatically than gizzard shad, most likely due to greater cyclopoid reduction by bluegill compared with gizzard shad. The simultaneous decrease in $>200 \text{ }\mu\text{m}$ PP and increase in $20\text{--}200 \text{ }\mu\text{m}$ PP may reflect the shift from copepods and cladocerans to rotifers whereas $12\text{--}20 \text{ }\mu\text{m}$ PP increased because rotifers cannot graze efficiently $12\text{--}20 \text{ }\mu\text{m}$ particles (Bogdan and Gilbert 1984). The $<0.2 \text{ }\mu\text{m}$ PP was higher with bluegill than with gizzard shad.

A fish biomass $\times$ planktivore type interaction occurred for $20\text{--}200 \text{ }\mu\text{m}$ PP. Analysis of simple effects showed that at 30 and 50 g/m^3 , concentrations of $20\text{--}200 \text{ }\mu\text{m}$ PP were higher with gizzard shad than with bluegill ($P = 0.008$ and 0.09 , respectively).

Fish biomass and planktivore type did not have significant effects on periphytic chlorophyll *a* whereas we detected sig-

nificant declines in densities of chironomid tubes attached to tank sides with fish biomass. Densities of chironomid tubes were significantly lower with bluegill than with gizzard shad (Fig. 4). Bluegill visually locate and consume benthic prey (Werner 1977). Although gizzard shad of the size used in this study commonly consume sediments and detritus, benthic macroinvertebrates are not included in their diet probably because they do not visually locate individual prey (Mummert and Drenner 1986).

Our results are consistent with other studies suggesting that consumption of macrozooplankton by planktivorous fish results in the enhancement of rotifer densities (Vanni 1987b; Threlkeld 1988) and phytoplankton productivity and biomass (Shapiro et al. 1975; Carpenter et al. 1985, 1987). Suppression of cladocerans and cyclopoids may have permitted rotifers to increase because rotifers are not only outcompeted by *D. pulex* (Gilbert 1985; Vanni 1986), but also may be damaged or killed by the filtering apparatus of cladocerans (Gilbert 1985; Gilbert and Stemberger 1985), or even consumed by *Mesocyclops* (Williamson and Gilbert 1980). With lower grazing rates and narrower diet breadth (Neil 1984), rotifers permitted phytoplankton to increase.

Gizzard shad consume phytoplankton, but $130\text{--}160 \text{ mm}$ SL gizzard shad can only efficiently filter particles $>40 \text{ }\mu\text{m}$ as per interraker distances (Mummert and Drenner 1986; Drenner et al. 1986). Those phytoplankton too small to be grazed by gizzard shad (unicellular flagellates, unicellular green algae, and pennate diatoms ($<20 \text{ }\mu\text{m}$ in smallest dimension; maximum dimensions are shown on Fig. 2)) came to dominate mesocosms with shad because elongated particles can pass through filters, limited only by their smallest diameter (Runge and Ohman 1982). However, because of their globular shape, larger colonial green algae may have been suppressed by gizzard shad grazing at high biomass.

Fish also influence phytoplankton via alteration of nutrient cycles (Nakashima and Leggett 1980; Vanni 1987a; Threlkeld

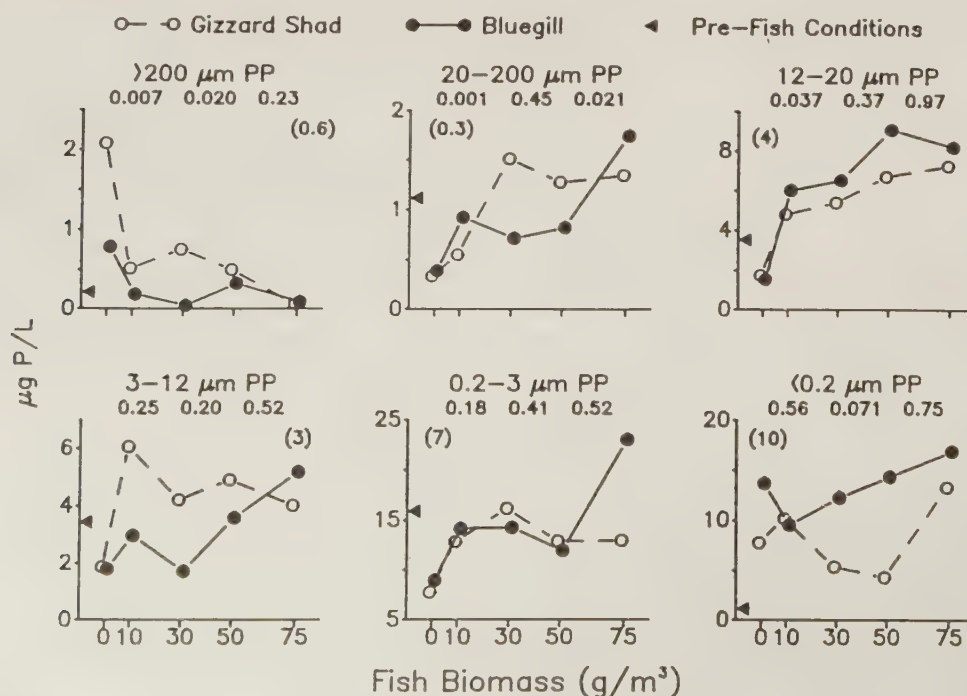


FIG. 3. Mean responses of size fractions of PP on two sampling dates (days 14 and 28) after fish introduction to fish biomass and planktivore type. Probability values from repeated-measures ANOVA, $\sqrt{\text{MS}}$ error, and evaluation of main and interaction effects, as in Fig. 2.

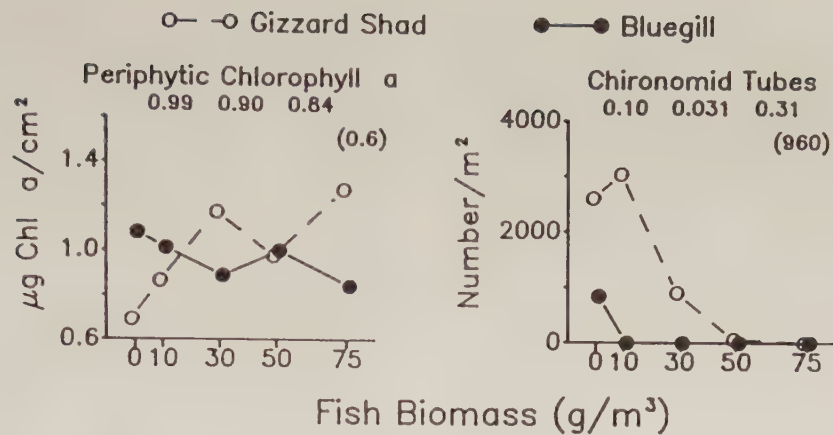


FIG. 4. Mean responses of periphytic chlorophyll *a* and chironomid tubes density (day 28) to fish biomass and planktivore type. Probability values from two-way ANOVA, $\sqrt{MS}$ error, and evaluation of main and interaction effects, as in Fig. 2.

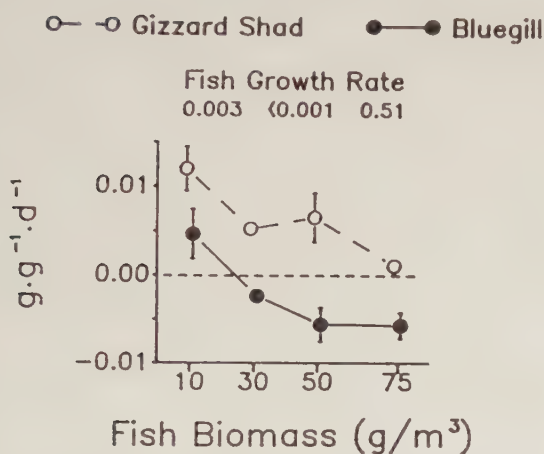


FIG. 5. Mean gizzard shad and bluegill growth rates (expressed in wet mass per stocked wet mass per day) across fish biomass levels (two replicates per treatment combination) between stocking and recovering dates (33–34 d). Vertical bars represent ± 1 SE. Probability values from two-way ANOVA, $\sqrt{MS}$ error, and evaluation of main and interaction effects, as in Fig. 2.

1988; Northcote 1988). Fish biomass did not influence TN, but TP increased with fish biomass (Fig. 2). Fish have complex effects on nutrient levels, excreting nutrients and altering nutrient cycles through predation (Vanni 1987a; Vanni and Temte 1990; Vanni et al. 1990). Fish can act either as nutrient sources or sinks depending on growth patterns (Threlkeld 1988). In our study, bluegill growth rates were lower than gizzard shad growth rates at all fish biomasses (Fig. 5). Gizzard shad always gained weight, but gizzard shad growth declined with fish biomass. Bluegill growth also declined with fish biomass, but bluegill only gained weight at 10 g/m³. Phytoplankton enhancement by bluegill may have, in part, resulted from nutrient release caused by loss of bluegill body mass (Threlkeld 1987), but we do not have information about changes in nutrient excretion by bluegill with weight loss to accurately estimate the nutrient loading.

One type of biomanipulation is the reduction of phytoplankton biomass (to increase water transparency) of lakes through reduction of planktivores, permitting herbivorous zooplankton to increase (Shapiro and Wright 1984; Carpenter et al. 1985). A critical question about this biomanipulation technique is whether partial suppression of planktivores by piscivores can

improve water quality (McQueen et al. 1986; Shapiro 1990). The answer partially depends on whether the fish biomass – phytoplankton biomass relationship is linear or sigmoid. If linear (Carpenter et al. 1985; McQueen et al. 1986), then reductions in planktivores at high biomass will produce improvements in water quality. If sigmoid (Drenner and Smith 1991), then reductions in planktivores at high biomass will not result in commensurate reductions in phytoplankton biomass.

In our study the fish biomass – chlorophyll *a* relationships were sigmoid. With bluegill, this relationship may be artificial because (1) biomass levels of 50 and 75 g/m³ are unrealistically high for bluegill in nature (Carlander 1977) and (2) nutrient release resulting from loss of bluegill body mass may have occurred at biomass > 10 g/m³. In contrast, gizzard shad grew at all biomass levels. Carrying capacity for gizzard shad exceeded that for bluegill because shad feed on phytoplankton and detritus in addition to zooplankton (Mummert and Drenner 1986). Our growth rate data are consistent with observations that in lakes and reservoirs, filter-feeding gizzard shad typically maintain higher biomass than visual-feeding bluegill (Carlander 1977; Aggus et al. 1979; Miranda 1983). Phytoplankton biomass increased with gizzard shad biomass in a sigmoid fashion, suggesting that reductions of gizzard shad between 75 and 10 g/m³ would produce less beneficial effects on chlorophyll than reductions of gizzard shad below 10 g/m³.

The success of any biomanipulation effort aimed at reducing phytoplankton biomass requires planktivores to be reduced sufficiently to permit zooplankton to increase and or nutrient loading by fish to decrease (Braband et al. 1990), but not so far as to threaten piscivore production (McQueen et al. 1986, 1990). Another type of biomanipulation is the stocking of forage fish to maintain piscivore production. Because water quality improvement and piscivore production enhancement are often contradictory goals, a trade-off between water quality and angler harvest might well be necessary under a biomanipulation program of lake management. Gizzard shad often dominates the forage fish biomass and is the primary prey of most piscivore species (Noble 1981), but it is currently difficult to predict how reductions in gizzard shad biomass (to improve water quality) might affect piscivore production. Partial removals of gizzard shad can have negative, neutral, or even positive effects on piscivore growth; however, most manipulations lacked a reference system and data were not statistically analyzed (DeVries and Stein 1990). Our chlorophyll data (see Fig. 2) suggest that

gizzard shad biomass must be reduced below 10 g/m³ (<200 kg/ha, on the basis of tank surface area) to achieve a significant reduction in phytoplankton biomass. This biomass of gizzard shad is lower than the typical biomass of gizzard shad in lakes and reservoirs (Aggus et al. 1979). Due to high fecundity and growth of gizzard shad (causing them to quickly reach a size refuge), the critical issue becomes whether a reduction in gizzard shad biomass below 10 g/m³ can be achieved and maintained for more than one season to ensure a lasting reduction in phytoplankton biomass without having a detrimental effect on piscivorous game fish.

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Revised Estimates of Age and Growth of the Sandbar Shark (*Carcharhinus plumbeus*) from the Western North Atlantic

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Age and growth of the sandbar shark (*Carcharhinus plumbeus*) were determined from tag and recapture data covering a 26-yr period (1964–90). Results were compared with previously published age and growth estimates based primarily on rings in vertebrae. Recent long-term tag returns suggest that the sandbar shark grows much slower than previously proposed and may take nearly 30 yr to reach maturity. Revised von Bertalanffy parameters (sexes combined) are $L_{\infty} = 186$, $k = 0.046$, and $t_0 = -6.45$. The limitations of ageing elasmobranchs solely from rings in vertebrae and the need for validating rings in hardparts of fishes are discussed.

On a déterminé l'âge et le taux de croissance du requin gris (*Carcharhinus plumbeus*) à l'aide de données d'étiquetage recueillies pendant une période de 26 ans (1964–1990). Les résultats ont été comparés avec des estimations antérieures de l'âge et du taux de croissance basées en grande partie sur le nombre d'anneaux dans les vertèbres. Les données récentes fournies par des étiquettes posées il y a plusieurs années portent à croire que le taux de croissance du requin gris est nettement moins élevé qu'il l'a été signalé et que l'espèce peut n'atteindre la maturité que vers 30 ans. Les paramètres révisés de von Bertalanffy (sexes combinés) sont comme suit : $L_{\infty} = 186$, $k = 0,046$ et $t = -6,45$. On examine aussi les limites qu'imposent la détermination de l'âge des élasmo-branches par lecture des anneaux des vertèbres et le besoin de valider les anneaux dénombrés sur les parties osseuses de poissons.

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In an earlier study of age and growth of the sandbar shark (*Carcharhinus plumbeus*) (Casey et al. 1985), age estimates were based on vertebral rings with additional evidence provided by tag and recapture data, length–frequency distributions, and sharks maintained in aquaria. Despite the attempt to support vertebral ring interpretation by these other methods, tag recoveries in subsequent years are evidence that the ages from vertebrae were underestimated.

In a survey of 500 published studies of age and growth in fishes, Beamish and McFarlane (1983) reported that ageing techniques were validated in less than 3% for all age classes and that "Use of inaccurate ages has caused serious errors in the management and understanding of fish populations." They further stated that "only by mark–recapture studies or use of known-age fish can all age classes in a population be validated. If such studies are not feasible, fish should be aged by several methods, and the possibility of errors in age estimates must be considered."

We decided to reexamine age and growth data for the sandbar shark in light of (1) studies that questioned the accuracy of conventional ageing methods, (2) the need for accurate age data for management plans that are imminent for Atlantic sharks, and (3) the additional growth information from tagged sharks that have been recaptured since 1983.

Materials and Methods

Tag–recapture data and vertebral samples were obtained in the same manner as in Casey et al. (1985). The present study

was based on data collected since the 1985 publication unless otherwise noted. Total length (TL) and fork length (FL) were measured to the nearest centimetre following the conventions of Bigelow and Schroeder (1948). All lengths are reported as FL. FL can be converted to TL using the following relationship:

$$FL = 0.8265 TL + 1.3774 \quad (n = 4250).$$

Vertebrae obtained from recaptured sharks were processed histologically as in Casey et al. (1985), except that RDO (DuPage Kinetics¹) was used as a decalcifying agent. Vertebral sections were "read" from an image projected on a Summagraphics MM-1812 digitizing tablet (Skomal 1990). Measurements from the focus to growth bands at points along the internal corpus calcareum were digitized directly into an IBM PC-XT computer. The criteria used to define a band followed Casey et al. (1985).

Vertebral samples from recaptured sharks that were measured at both tagging and recapture were used to validate the periodicity of the bands. The vertebral radius (VR) at the time of tagging was calculated by converting the measured FL to VR using the FL–VR relationship from Casey et al. (1985). The number of bands beyond this radius was then related to the known time at liberty.

A von Bertalanffy growth function (VBGF) for combined sexes was not calculated for the vertebral data in Casey et al.

¹Reference to trade names does not imply endorsement by the United States Government.

TABLE 1. Tag returns from *C. plumbeus* measured at tagging and recapture (at liberty 359 d to 25 yr). YR = yellow rototag; RR = red rototag; M, A = "M" dart tag; N = 33

Size class (cm)	Tag type	Tag No.	Sex	Date (mo/d/yr)		Days free	Fork length (cm)			Growth per year (cm)	Mean Growth (cm)	SD
				Tag	Recapture		Tag	Recapture	Growth			
50–69	YR ^a	128	M	07/16/65	08/17/67	762	63	75	12	5.8	5.2	0.78
	RR ^a	951	F	06/15/66	05/08/68	693	69	78	9	4.7		
70–79	RR ^a	995	M	06/16/66	08/25/67	435	74	83	9	7.6	5.4	3.04
	YR	136	M	07/16/65	03/27/86	7559	76	145	69	3.3		
80–89	RR ^a	747	F	06/22/65	06/18/70	1822	80	99	19	3.8	4.7	3.03
	RR ^a	410	F	06/19/65	06/22/70	1829	81	106	25	5.0		
	YR ^a	1373	M	06/09/69	06/21/71	742	83	103	20	9.8		
	RR ^a	219	M	07/29/64	05/28/68	1399	86	89	3	0.8		
	YR ^a	471	F	06/18/66	06/16/69	1094	86	98	12	4.0		
	RR	654	F	06/14/66	11/06/86	7450	87	119	32	1.6		
	RR ^a	798	M	06/23/65	08/08/67	776	88	98	10	4.7		
	RR ^a	930	F	06/25/65	08/25/68	1157	89	115	26	8.2		
	RR ^a	930	F	06/25/65	08/25/68	1157	89	115	26	8.2		
90–99	YR ^a	1219	F	08/10/68	07/05/70	694	91	102	11	5.8	4.6	1.62
	YR ^a	330	F	06/17/66	06/20/67	368	92	95	3	3.0		
	RR ^a	962	M	06/15/66	08/08/73	2611	93	138	45	6.3		
	RR ^a	714	M	06/22/65	09/12/66	447	94	102	8	6.5		
	RR	736	F	06/22/65	07/06/90	9145	94	157	63	2.5		
	YR ^a	884	M	08/01/67	08/28/68	393	95	101	6	5.6		
	RR ^a	894	F	06/24/65	08/05/68	1138	95	112	17	5.5		
	RR	691	M	06/20/65	10/07/86	7779	96	157	61	2.9		
	M	52016	M	11/03/79	04/27/89	3463	97	129	32	3.4		
100–109	A	8335	F	08/24/83	08/17/84	359	100	100	0	0	5.6	4.90
	YR ^a	375	F	06/17/66	06/26/67	374	101	105	4	3.9		
	RR ^a	435	F	06/20/65	08/31/66	437	101	111	10	8.4		
	RR ^a	758	M	06/22/65	10/04/66	469	102	118	16	12.5		
	RR ^a	369	F	06/19/65	08/25/68	1163	104	114	10	3.1		
110–119	M	99882	M	05/12/84	07/05/87	1149	112	115	3	1.0	1.0	—
120–129	M	114666	M	10/16/86	01/24/90	1196	120	127	7	2.1	2.1	—
140–149	M	39393	F	09/25/82	02/14/88	1968	140	152	12	2.6	6.0	3.6
	M	114657	F	10/15/86	03/10/90	1242	143	176	33	9.7		
	M	111582	M	11/16/85	05/17/89	1278	147	167	20	5.7		
150–159	M	115001	M	08/30/87	08/18/89	719	152	157	5	2.6	2.6	—
160–169	M ^a	19399	F	03/13/73	03/27/76	1110	164	168	4	1.3	1.3	—

^aFrom Casey et al. (1985, table 3).

(1985). Using the data in their table 3 ($n > 5$) and using FISH-PARM (Prager et al. 1987), we calculated von Bertalanffy parameters for the combined sexes to compare with our tag-recapture VBGF.

Only sharks that were measured at time of tagging and recapture and at liberty for ≥ 365 d were included in the tag-recapture data set. The von Bertalanffy growth parameters L_{∞} and k were calculated from the tagging data using Fabens' (1965) model. T_0 was calculated using the following equation:

$$t_0 = t + 1/k[\ln(L_{\infty} - L_t)/L_{\infty}]$$

where L_t = known length at age (size at birth), k = the von Bertalanffy growth constant, and L_{∞} = the theoretical maximum attainable length from the von Bertalanffy growth equation. The VBGF and curves produced from vertebral and tag-recapture data were then compared.

Growth per year values, from the tagging data in Casey et al. (1985, table 3), were plotted additively from fish in the 50–110 cm FL size range to compare growth rates between the two studies. Data from sharks larger than 110 cm were not used due to the gap in recapture data between 110 and 150 cm. The final growth curve was based on all tag-recapture data.

Results

New growth information on 12 recaptured sandbar sharks obtained between 1983 and 1990 was combined with data from 21 recaptures listed in Casey et al. (1985, table 3) to produce values for L_{∞} and k of the VBGF (Table 1). Our revised von Bertalanffy parameters for the sandbar shark are $L_{\infty} = 186$, $k = 0.046$, and $t_0 = -6.45$ (Fig. 1). T_0 was calculated based on an average size at birth of 47.7 cm (Casey et al. 1985). A von Bertalanffy curve fit to the vertebral data (combined sexes) from Casey et al. (1985) consists of the following parameters: $L_{\infty} = 303$, $k = 0.039$, and $t_0 = -3.92$. The current tag-recapture VBGF and the growth per year data from Casey et al. (1985) both estimate slower growth and greater longevity for the sandbar shark than that previously estimated from vertebral data (Table 2; Fig. 1).

A vertebral sample was obtained from one recaptured shark which was at liberty for longer than 1 yr. This shark (No. M 114666) was at large for 1196 d (3.3 yr) and showed growth of 2.1 cm/yr. The specimen measured 120 cm at release and 127 cm at recapture. The ring count and measurements from

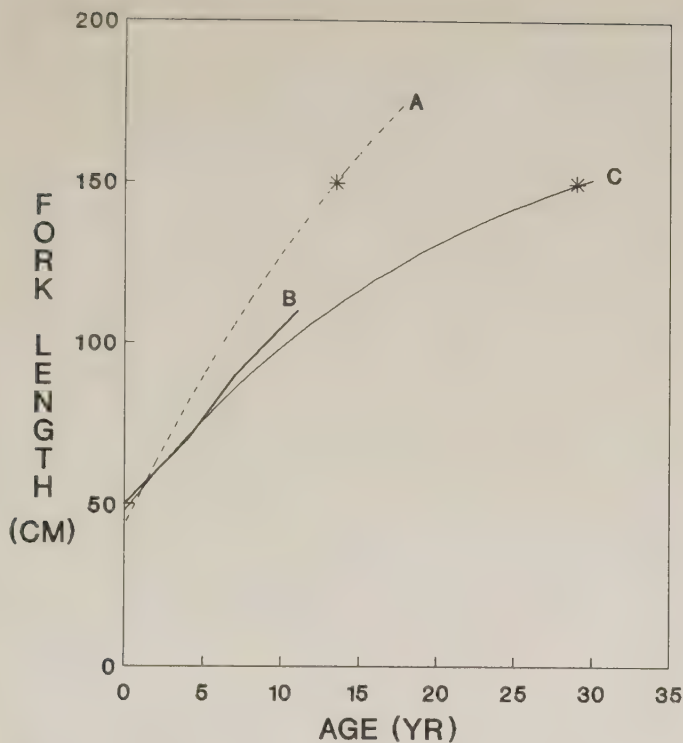


FIG. 1. Estimated growth for *C. plumbeus* with a von Bertalanffy growth curve based on (A) back-calculation of size at age from rings in vertebrae, $n = 442$, (B) growth-per-year data based on tag-recapture data from Casey et al. (1985, table 3), $n = 21$, and (C) a von Bertalanffy growth curve based on all tag-recapture data, $n = 33$ (Table 1). The asterisk denotes estimated size and age at maturity.

TABLE 2. Comparison between von Bertalanffy parameters derived from vertebral data and tag-recapture data.

	L_{∞}	k	t_0	N
Tag-recapture	186	0.046	-6.45	33
Vertebral (sexes combined)	303	0.039	-3.92	447

the vertebral section showed two, rather than the expected three, rings past the tagging radius.

Three recaptures provide detailed examples of the longevity of this species. (1) In 1985, a female sandbar shark (No. M 3868) that was at liberty for 17 yr was shipped to the NMFS Laboratory at Narragansett, RI. This shark was estimated to be 102 cm in length at tagging and measured 155 cm at recapture. Using the vertebrally derived VBGF, it was estimated to be 5 yr old at tagging and at least 22 yr old at recapture. Examination of its reproductive organs revealed that the individual was still immature. (2) In 1990, a female sandbar shark (No. RR 736) was recaptured after 25 yr at liberty. This individual, measured by a NMFS biologist, was 112 cm in length when tagged and released in 1965 and measured 157 cm at recapture. The estimated age at tagging (7 yr) gives this shark an age of 32 yr at recapture. (3) A male sandbar shark (No. M 3030) measured 185 cm FL at tagging was recaptured after 10 yr. Since the length at first maturity is 150 cm (Fig. 1), it is reasonable to assume that this individual was over 30 yr old at tagging and over 40 yr at recapture.

Discussion

Casey et al. (1985) compared vertebral ring counts with tag-recapture data, aquarium studies, and length-frequency distri-

butions to obtain a growth curve for the sandbar shark. Despite this multiple approach to age and growth, the study substantially underestimated the age of the sandbar shark. The principal reason for the difference between the present and past studies is the reliance on vertebral rings in the 1985 work. The vertebral data were emphasized because these were based on information from over 400 precisely measured sharks with distinct vertebral rings. At that time the tag-recapture information was considered less reliable because much of it was based on estimated size data. Moreover, growth reflected in some of the early tag returns was so slow that it was easy to acquire a bias against the tagging data. Consequently, the focus of the age and growth work was directed toward interpreting vertebral rings and supporting the estimates with tag-recapture and length-frequency data. However, in the discussion section the authors suggested that they may have underestimated the ages of large sandbar sharks due to the "... large number of rings near the margin that could be interpreted as year marks." These marks were not counted, as they did not fit the criteria for an annual mark as validated in the younger size classes (Casey et al. 1985). The authors also presented data from recaptured sharks that suggested older ages at maturity and a higher maximum age than estimated from the vertebrae. Since that publication, additional recapture data on larger fish and fish at liberty for longer time periods have been obtained that strengthen the case for using tagging data. These and earlier data presented by Casey et al. (1985, table 3) on growth in recaptured sandbar sharks show a markedly slower growth rate than that derived from vertebral rings. A von Bertalanffy growth curve based on the first 21 sandbar sharks measured at both tagging and recapture and at liberty for ≥ 1 yr estimates an age at first maturity (based on 150 cm) of 21 yr. The evidence from tagging presented both here and in Casey et al. (1985) indicates that most sandbar sharks very likely do not mature until they are in their late twenties. The curve presented in the current study utilizing the original 21 recaptures plus the 12 additional recaptures suggests a slower growth rate after age 5-6 (Fig. 1) and an age at maturity of 29-30 yr.

The maximum age of the sandbar shark is difficult to estimate. The NMFS tagging program has received data from recaptures of four sandbar sharks at liberty exceeding 21 yr. However, by following criteria for vertebral rings the highest ring count attained by Casey et al. (1985) for fish of similar size was 21. This lends additional support to the suggestion that ages are underestimated by vertebral counts. Additional tagging of large adults is needed to strengthen current estimates of longevity. Nevertheless, it is not unreasonable now to suggest that sandbar sharks can live for over 50 yr.

Although vertebral rings from juvenile sandbar sharks up to 112 cm have been validated as annual using both tag-recapture results combined with vertebral data and vertebrae from tetracycline-injected captive specimens (Casey et al. 1985; Branstetter 1987), validation of annual rings in young fish cannot be extended to all age classes (Beamish and McFarlane 1983). In discussing rings in skeletal structures, Beamish and McFarlane (1983) concluded "... when growth is reduced ... it is possible, even probable, that there will be a change in the appearance of an annulus and that the method of age determination will have to be modified. Only by validating the method [for older fish] can it be proven that fish are not older than estimated and that older fish are not an important component of the population." This appears to be the case in the sandbar shark. Evidence from both tag-recapture data and a change in the deposition pattern of vertebral rings past ring numbers six

to seven suggest that the outer rings are at best difficult to read and at worst may not be annual in adult sandbar sharks. It is possible that the outer rings reflect changes in life history patterns (i.e. migrations in males, or alternate-year pupping in females). It has been demonstrated in skates that bands are not deposited during an active reproductive stage (Natanson 1990), and in angel sharks, bands appear to be deposited to strengthen the vertebral column and are not related to time (Natanson and Cailliet 1990).

The suggestion that rings in hardparts may not be a reliable method for aging fish throughout all age classes is not unique. Beamish and Harvey (1969) used several hardparts and tag-recapture analysis to obtain age estimates for the white sucker. Their results indicate that rings in hardparts were deposited annually up to age 5 but after that could lead to underestimations of age by as much as 5 yr in fish over 8 yr old. Prince et al. (1986) concluded that dorsal fin spine analysis in sailfish was accurate between ages 1 and 5 but that it probably underestimated the maximum ages by "...a considerable margin."

Our reexamination of age in the sandbar shark again brings up the need for validation of all age classes as discussed by Beamish and McFarlane (1983) and more recently by Gauldie (1990). The use of unvalidated vertebral rings in adult sandbar sharks underestimated the size at maturity by at least 8 and possibly 16 yr. In a large, slow-growing species with low fecundity and alternate-year pupping, this will make a substantial difference in calculating the theoretical maximum output of young, which is a major consideration in any attempt to manage the species.

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Behaviour, Habitat Use, and Movements of Coho Salmon (*Oncorhynchus kisutch*) Smolts during Seaward Migration¹

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McMahon, T. E., and L. B. Holtby. 1992. Behaviour, habitat use, and movements of coho salmon (*Oncorhynchus kisutch*) smolts during seaward migration. *Can. J. Fish. Aquat. Sci.* 49: 1478–1485.

Coho salmon (*Oncorhynchus kisutch*) smolts formed aggregations in pools with large woody debris during their migration downstream and into the Carnation Creek estuary, British Columbia. Smolts utilized the estuary throughout the smolt run, with periods of high outmigration coinciding with spring tides which brought warmer, more saline water into the estuary. Smolt abundance in the stream and estuary was positively related to debris volume, and 82% of the 1260 smolts observed during underwater counts occurred within 1 m of debris. Debris volume and smolt density were significantly lower in clearcut than in buffered stream sections. Our observations support the need to retain and manage large woody debris for smolt habitat in streams and estuaries.

Des saumoneaux cohos (*Oncorhynchus kisutch*) se sont regroupés dans des fosses encombrées de gros morceaux de bois lors de la dévalaison vers l'estuaire du ruisseau Carnation, en Colombie-Britannique. Ils ont fréquenté cet estuaire pendant toute la durée de la dévalaison; un grand nombre l'ont quitté lors des marées de vives-eaux qui baignaient l'estuaire d'eau plus chaude et plus salée. L'abondance des saumoneaux dans le cours d'eau et l'estuaire était en corrélation positive avec le volume de morceaux de bois; ainsi, 82% des 1 260 saumoneaux observés au cours de dénombrements sous-marins étaient retrouvés en deçà de 1 m de débris de bois. Le volume de débris et la densité des saumoneaux étaient nettement inférieurs dans les tronçons du cours d'eau où les rives avaient été coupées à blanc que dans les tronçons où une marge tampon existait. Nos observations confirment qu'il est nécessaire de garder de gros morceaux de bois dans les cours d'eau et les estuaires afin qu'ils servent d'habitat aux saumoneaux.

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Parr-smolt transformation in coho salmon (*Oncorhynchus kisutch*) and other anadromous salmonids is accompanied by distinct changes in morphology, physiology, and behaviour (Hoar 1976; Wedemeyer et al. 1980). While the morphological and physiological changes that occur have been well documented, relatively few studies have examined behavioural changes during the shift from freshwater to marine habitats. Laboratory observations by Hoar (1951) suggested that during smoltification, coho salmon show a marked decline in aggression and associated territorial and hierarchical behaviour and form aggregations presumably adaptive for life in schools in the open ocean. In contrast, Mason (1966) and Paszkowski and Olla (1985) found that smolts continue to exhibit aggression and hierarchical behaviour in seawater. No direct underwater observations of coho smolts in the field have been reported to corroborate laboratory observations.

Prior to seaward migration, presmolts overwinter in protected sites of deep pools and undercut banks containing large woody debris (Bustard and Narver 1975; Tschaplinski and Hartman 1983), off-channel ponds, wetlands, sidechannels, and low-gradient tributaries (Peterson 1982; Brown and Hartman 1988), and lakes (Swales et al. 1988). Bustard and Narver (1975) and Tschaplinski and Hartman (1983) found that coho overwintering in off-channel sites moved back to the main channel of Carnation Creek, British Columbia, in early spring, up to 6 wk prior to the main period of smolt migration. How-

ever, the types of habitat utilized by coho salmon prior to and during the period of smoltification and migration to the sea have not been previously described.

Estuaries may be important for smolts as sites for completion of seawater adaptation and other smoltification processes (Iwata and Komatsu 1984; McCormick et al. 1985). Some species, notably chinook (*O. tshawytscha*) and chum salmon (*O. keta*), may spend several months in estuaries utilizing the abundant food resources there prior to moving out to sea (Healey 1982; Mason 1974; Macdonald et al. 1987; Murphy et al. 1988). Studies have shown that coho salmon parr utilize estuaries during spring and summer (Murphy et al. 1984; Tschaplinski 1988), but information is limited on estuarine utilization by coho smolts, particularly wild fish.

In this study we describe the behaviour, movement timing, and habitats utilized by wild coho salmon smolts prior to and during their migration downstream into the Carnation Creek estuary. We show that smolts are closely associated with large woody debris during seaward migration and discuss the implications of this association to habitat management for the species.

Methods and Materials

Carnation Creek empties into Barkley Sound on the west coast of Vancouver Island. The stream is ~8 km long of which the lower 3.2 km is accessible to anadromous salmonids. Coho salmon are the predominant salmonid rearing in the stream. The watershed is the site of a long-term study initiated in 1970 to

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examine the effects of logging on a coastal rainforest stream. Physical and biological characteristics of the stream have been described in detail elsewhere (Hartman and Scrivener 1990).

Three distinct sections of the watershed were delineated for this study: (1) a small, 500-m-long, "riverine-type" estuary bounded on its upper end by a permanent fish counting fence located near the uppermost limit of tidal influence and its lower end by Barkley Sound, (2) a "buffered" section (0–1300 m upstream from the counting fence) where a strip of trees was left intact along the stream margin after logging of 41% of the watershed during 1976–81, and (3) a "clearcut" section (1300–3200 m above the fence) where streamside trees had been removed during logging and much of the instream woody debris removed or lost during logging and subsequent freshets (Tschaplinski and Hartman 1983; Hartman and Scrivener 1990).

Eight 50-m-long study reaches were chosen to represent the characteristics of each section. In the estuary, a study reach was designated in the upper, middle, and lower part of the estuary based on differences in woody debris, streamside canopy, and salinity patterns (Table 1). Buffered and clearcut reaches were located downstream or adjacent to the mouths of off-channel ponds and tributaries utilized by coho salmon as overwintering sites (750, 1600, and 2600 m upstream from the main counting fence; Brown and Hartman 1988). Together, the eight study reaches comprised 30% of the total area of the estuary and 8% of the stream. Additional observations were made in Dicks Creek, a small tributary entering the estuary about 100 m below the main fish fence (see map, Bustard and Narver 1975).

Behaviour and habitat use by coho salmon smolts were determined from underwater counts and observations using a wet suit, mask, and snorkel. Dives were made at least biweekly at times between 1000 and 1500 h in each of the eight study reaches during March–June 1985. Temperatures during this

period ranged from 4 to 10°C. Dives were limited to high-visibility (>3 m) conditions, i.e. stream discharges <0.5 m³/s and low tides.

Observations were made by entering the downstream end of a study reach and slowly swimming upstream in a zigzag fashion through the entire reach. Fish could be approached quite closely (within 1 m) and were readily counted and observed. When fish were encountered, a diver made repeated counts over a 10-min period to insure as complete a count as possible. Counts of smolts located within dense cover were often facilitated by fish swimming out of cover to feed on benthic organisms purposely dislodged by the diver. Feeding, aggression, and aggregative behaviour were also noted. Following the definition of Cunjak and Power (1986, p. 1972), an aggregation was defined as "a group of (5 or more) fish in close association. . . , displaying a common behavioural pattern but lacking the spatial homogeneity and polarity of schooling fish." The number and location of fish were recorded on a map of the study site by an assistant on the bank. Smolts were distinguished from parr based on their size and colouration (McMahon and Hartman 1988). Distance of fish from cover was estimated within 1 m by the diver and later measured in relation to particular stream features noted during a dive. Four separate repeat counts of a study reach on the same or next day indicated that precision of visual estimates was ~10–15%. Accuracy of counts was not measured. However, previous comparisons of visual counts with pole-seine/electrofishing removals of juvenile coho salmon in Carnation Creek in sites similar to those used in the present study indicated that visual counts of coho were about 15% lower than removal estimates (Tschaplinski and Hartman 1983).

Physical habitat features of study reaches were mapped on the basis of 11 transects positioned 5 m apart along each reach. Habitat type (pool, riffle, or glide) and water depth were determined at 1-m intervals along each transect. Current velocity

TABLE 1. Physical habitat characteristics of the eight study reaches in Carnation Creek. All reaches were 50 m in length.

Location	Distance from fence (m)	Area (m ²)	Mean (max.) depth (m)	Pools/ glides/ riffles (%)	Woody debris				Site characteristics		
					Total vol. (range) (m ³)	Area (m ²)	No. of jams	Bank cover (m ²)	Canopy (%)	Vegetation	Salinity (ppt)
Clearcut											
A	1500	305	0.3 (1.4)	24/18/58	4.6 (0.2–4.4)	6.9	2	7.3	<10	Young alder and salmonberry	
B	1550	490	0.4 (1.2)	49/14/37	0.9 (0.1–0.8)	6.6	2	39.7	<10	Young alder and salmonberry	
C	1625	425	0.4 (1.1)	37/26/37	9.9 (—)	14.1	1	50.6	<10	Young alder and salmonberry	
Buffered											
A	530	465	0.4 (1.6)	36/36/28	25.4 (0.5–19.1)	20.7	4	50.2	~75	Mature forest	
B	630	545	0.5 (1.5)	53/24/23	29.6 (2.0–14.5)	39.2	4	52.3	~75	Mature forest	
Estuary											
Upper	–10	510 ^a	0.6 (1.8) ^a	52/19/29	34.9 (1.3–33.6)	31.8	2	43.9	~75	Mature forest	0–5 ^b
Middle	–60	420 ^a	0.6 (1.2) ^a	74/9/17	1.3 (—)	1.2	1	43.3	<20	Salt marsh, brush cover along one bank	0–5 ^c
Lower	–405	605 ^a	0.4 (1.6) ^a	32/24/44	21.2 (—)	14.1	1	0	<10	Salt marsh (<i>Spartina</i> sp.)	10–22

^aAt low tide.

^b≥10 ppt only during spring tides.

^c≥10 ppt only during high tides.

was measured with a Gurley Pygmy meter in areas inhabited by coho salmon smolts. Bank cover was measured with a tape and included overhanging vegetation and undercut banks. Woody debris cover was defined as the volume of water containing debris cover and determined by measuring the surface area and depth of a woody debris accumulation (Tschaplinski and Hartman 1983). Salinity and water temperatures were measured in the estuary following each census.

Movements of smolts from three tributaries used as overwintering sites were determined from small two-way fences erected near the tributary junctions with the main channel (Brown and Hartman 1988). Movements of smolts into the estuary were monitored at the main fish counting fence located near the upper limit of the Carnation Creek estuary (Andersen 1987). Potential triggers for seaward migration were examined by comparing smolt numbers at the main fish fence with stream discharge, water temperature, and lunar phase. Water temperature and stream discharge were recorded continuously at the hydrological weir located 500 m above the main fish counting fence.

Results

Downstream Movement

Movement of smolts began with the onset of emigration from upstream tributaries in late March and generally progressed over time in a downstream direction. The median date of emigration from tributaries (April 11) preceded peak counts of smolts in the buffered section (April 24), which in turn preceded the median date of the smolt run at the main fish fence (May 4) by about 10 d (Fig. 1). Smolts were present in the estuary below the fence throughout the smolt run, with peak counts lagging about 10 d behind the median date of migration at the fence. Most smolts had migrated from the estuary by early June.

The number of smolts (3-d average) migrating through the main fence was not influenced strongly by stream discharge ($r = 0.43$, $P = 0.12$). Temperatures during the main period of migration ranged from 6.5 to 8.5°C, with the number of migrants increasing significantly during declines in temperature ($r = -0.60$, $P = 0.02$). There was no significant trend between smolt numbers at the main fence and lunar phase (2-wk periods surrounding new and full moons) (Fig. 1C; $t = 1.79$, $P = 0.08$).

Sharp declines (high outmigration) in numbers of smolts in the estuary were associated with spring tides occurring during new and full moons (Fig. 1D). During three spring tidal cycles, smolt densities declined an average of $85.7 (\pm 4.6)\%$ compared with an average increase of $344.0 (\pm 70.6)\%$ during neap tides; this difference was highly significant (arcsine transformation, $t = 6.3$, $P = 0.003$). Incursions of warmer ($+2$ – 5°C), more saline (>20 ppt) water into the upper estuary accompanied spring tides (Table 1).

Relative Distribution and Habitat Use

Smolt density differed significantly ($P < 0.05$) (Kruskal–Wallis), between the three sections of Carnation Creek (Fig. 2). Few smolts were observed during underwater surveys in the clearcut section prior to and during the smolt run, despite emigration of 96 coho from adjacent or upstream tributaries (Fig. 1). Smolt density was about five times higher in the buffered section, where numbers increased after emigration from an adjacent tributary (Fig. 1B). Highest densities occurred in the estuary, where a total of 534 smolts were observed in aggregations of up to 136 fish (Fig. 1D).

Smolt densities were similar between study reaches within clearcut and buffered sections, but varied considerably between reaches and over time in the estuary (Table 2). No smolts were observed in the middle estuary reach compared with the relatively high utilization observed in upper and lower reaches. Use of the upper and lower reaches also varied: smolts utilized the upper estuary throughout the run whereas the lower estuary was utilized primarily in the latter half of the run (Table 2). In contrast with upstream reaches, no juvenile coho salmon were observed overwintering in the estuary prior to seaward migration (Fig. 1).

Large woody debris influenced the abundance of smolts in the stream and estuary. Smolt density was positively correlated with the total volume of large woody debris in a 50-m reach (Fig. 3A). Smolt density within 1 m of debris was also correlated with volume of individual debris jams (Fig. 3B), although this relationship was more variable and accounted for only 25% (r^2) of the variation in smolt density. The clearcut section had significantly less debris volume than did the buffered (5.2 ± 2.6 versus $27.5 \pm 3.0 \text{ m}^3$; $t = 6.0$, $P = 0.01$) (Fig. 3A; Table 1). Similarly, the middle estuary reach had little debris (Fig. 3A; Table 1) and no smolts (Table 2) compared with upper and lower estuary sites. Smolt density was not significantly associated with other habitat features such as debris area, bank cover, percent canopy, percent pools, and mean or maximum depth ($P > 0.20$; Table 1).

Smolt distribution was also highly clumped around debris. Over 80% of the 1260 smolts observed in Carnation Creek and Dicks Creek were within 1 m, and 95% within 2 m, of debris (Fig. 4). The distance between the 17 debris jams located in the eight study reaches averaged 21 m (range 5–50 m); the total area of these structures comprised about 3.5% of the total surface area surveyed (Table 1). These sites were characterized by deep (>1 m), slow-moving (<15 cm/s) water, overhead shade (low light intensity), and structurally complex cover afforded by root masses, deeply undercut banks, and submerged logs. Most smolts were observed in proximity to debris with volumes $>14 \text{ m}^3$ (Fig. 3B). Smaller accumulations and single logs generally supported few fish; the exception was the relatively high density of smolts observed near a small debris jam in the clearcut section where total debris was low (Fig. 3B). Smolts were notably scarce in areas affording deep pools or bankcover (e.g. clearcut and middle estuary reaches; Table 1) but lacking in large debris.

Behaviour

About 95% of smolts observed were aggregated in groups of >5 fish. Aggregation size increased significantly over the course of the smolt run and was significantly greater in the estuary than in the combined upstream sections (Table 3).

Smolts exhibited few agonistic interactions other than occasional nipping and chasing. Typically, fish were quite secretive, milling about in dark, low-velocity areas under cover with occasional forays to the edge of cover to feed on invertebrate drift or coho fry. Three instances of smolt predation on coho fry, one in the estuary and two in freshwater, were noted during snorkle surveys. Smolts exhibited a high degree of cohesiveness, moving together as a group if disturbed. Departures from this general pattern, however, indicated a degree of plasticity in behaviour. On several occasions, hierarchial behaviour, similar to that described by Paszkowski and Olla (1985), was observed among small numbers (≤ 5) of smolts vigorously defending feeding territories for short periods near the head of pools.

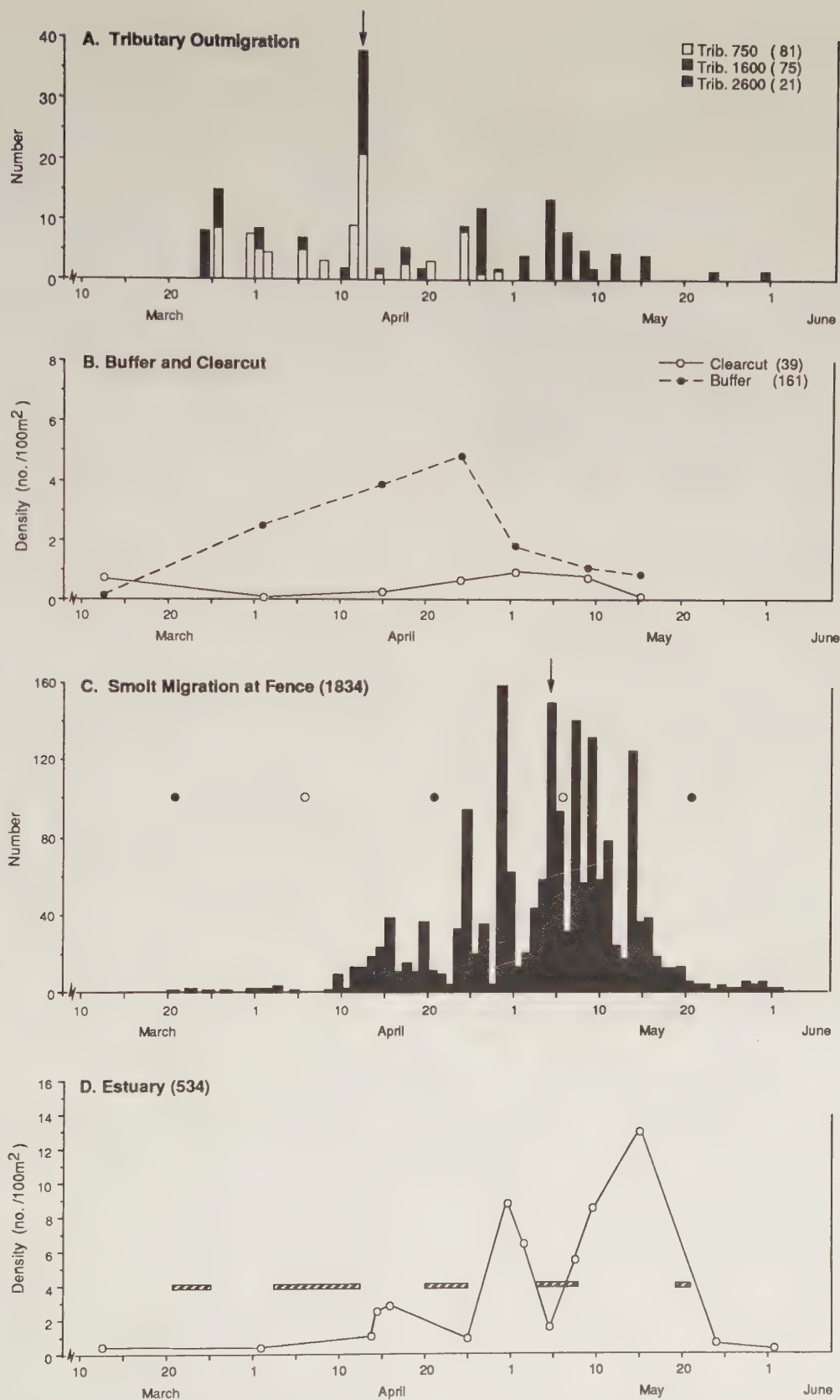


FIG. 1. Timing of movements and utilization of various sections by smolts in Carnation Creek during seaward migration. (A) Movement from upstream tributaries; tributary numbers refer to distance from the main fish fence; (B) density of smolts censused during snorkle counts in clearcut and buffer sections; (C) timing of downstream migration at the main fish counting fence located near the mouth of Carnation Creek; lunar phase indicated as full moon (open circles) and new moon (solid circles); (D) density of smolts censused during snorkle counts in the estuary below the fence; horizontal bars indicate spring tides >3.8 m. Vertical arrow indicates median dates of migration. Total number of smolts indicated in parentheses.

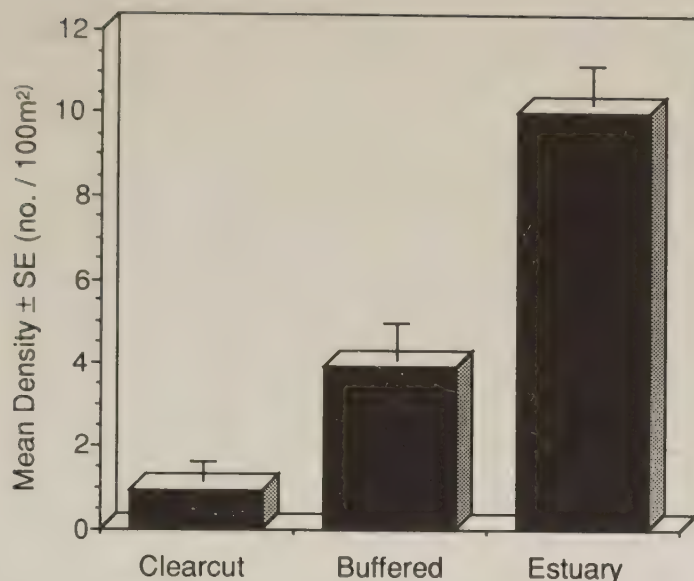


FIG. 2. Mean densities of smolts in clearcut, buffered, and estuary sections as calculated from three highest counts. Differences were significantly different ($P < 0.05$) among all three sections (Tukey's multiple comparisons test).

Discussion

Coho salmon juveniles formed aggregations near large woody debris in freshwater and estuarine sections of Carnation Creek during the period of parr-smolt transformation and seaward migration. Large aggregations of smolts have been reported beneath docks in Oregon estuaries (McAllister 1988). Moser et al. (1991) noted that smolts congregated for extended periods in areas of a Washington estuary having low water velocity and log pilings. These observations of smolts in the field are in agreement with Hoar's (1951) laboratory findings of strong aggregating and cover-seeking behaviours in smolts.

The results were not consistent with studies suggesting that a social system based on agonistic behaviour characterizes coho salmon following smoltification and entry into seawater (Mason 1966; Paszkowski and Olla 1985). We did observe aggression

among smolts (see also Hoar 1951, p. 257), but territorial-hierarchical interactions were infrequent and short-lived. Paszkowski and Olla (1985) suggested that contrasting observations of smolt behaviour may be attributable to aggression becoming more pronounced upon seawater entry. However, the highly clumped distribution and large size of aggregations of smolts we observed in the Carnation Creek estuary indicated that aggregative behaviour of smolts persists at least in brackish water. Our observations support Paszkowski and Olla's (1985) conclusion that smolts do not rigidly form schools but exhibit a degree of plasticity in behaviour dependent upon environmental conditions. The territorial behaviour we observed occasionally among small numbers of smolts feeding near the head of pools, where drift rates of invertebrates were presumably high (Smith and Li 1983), suggests that the combination of small group size and an abundant, localized food source, conditions similar to those provided in laboratory environments, may favour the expression of aggressive behaviour and development of feeding territories (Ryer and Olla 1991). The similarity in behaviour of smolts and lake-rearing coho salmon parr (Swain and Holtby 1989) likely reflects selection for a common behavioural pattern adaptive to open-water environments.

Aggregating and cover-seeking behaviour of smolts represents a continuation of, rather than a marked shift from, behaviour of coho salmon parr during winter. In winter, aggression declines and coho form aggregations near cover as temperatures decrease below 7°C (Bustard and Narver 1975; Tschaplinski and Hartman 1983; McMahon and Hartman 1989). We did not observe a return to territorial behaviour and a more dispersed distribution common to stream-dwelling coho during summer (Dill et al. 1981) as temperatures rose above 7°C in the spring, which suggests that behaviour of smolts was not solely under temperature control (Holtby et al. 1989).

Habitat utilization by smolts also parallels that of overwintering parr. In Carnation Creek, Bustard and Narver (1975) and Tschaplinski and Hartman (1983) showed that during winter, stream-dwelling coho occupy deep pools and undercut banks containing woody debris and are generally absent from habitats lacking cover. We observed a similar habitat use pattern by smolts. We also found a marked reduction in apparent carrying

TABLE 2. Comparisons of smolt density in eight 50-m study reaches and of the relative percentage of total density of smolts observed in the upper, middle, and lower estuary during the first (March 30 – May 3) and second half (May 4 – June 2) of the smolt run. n = total number counted; *differences in means significant at the $P < 0.05$ level; ns = not significant.

	Mean density (SE) (no./100 m ²)	n	% of total density	
			First half	Second half
Clearcut				
A	0.4 (0.2)	7		
B	0.2 (0.2)	7		
C	1.0 (0.3) ns	25		
Buffered				
A	2.9 (0.8)	82		
B	2.4 (0.8) ns	79		
Estuary				
Upper	8.4 (3.1)	260	93.5	53.9
Middle	0	0	0	0
Lower	7.5 (3.9)*	274	6.5	46.1

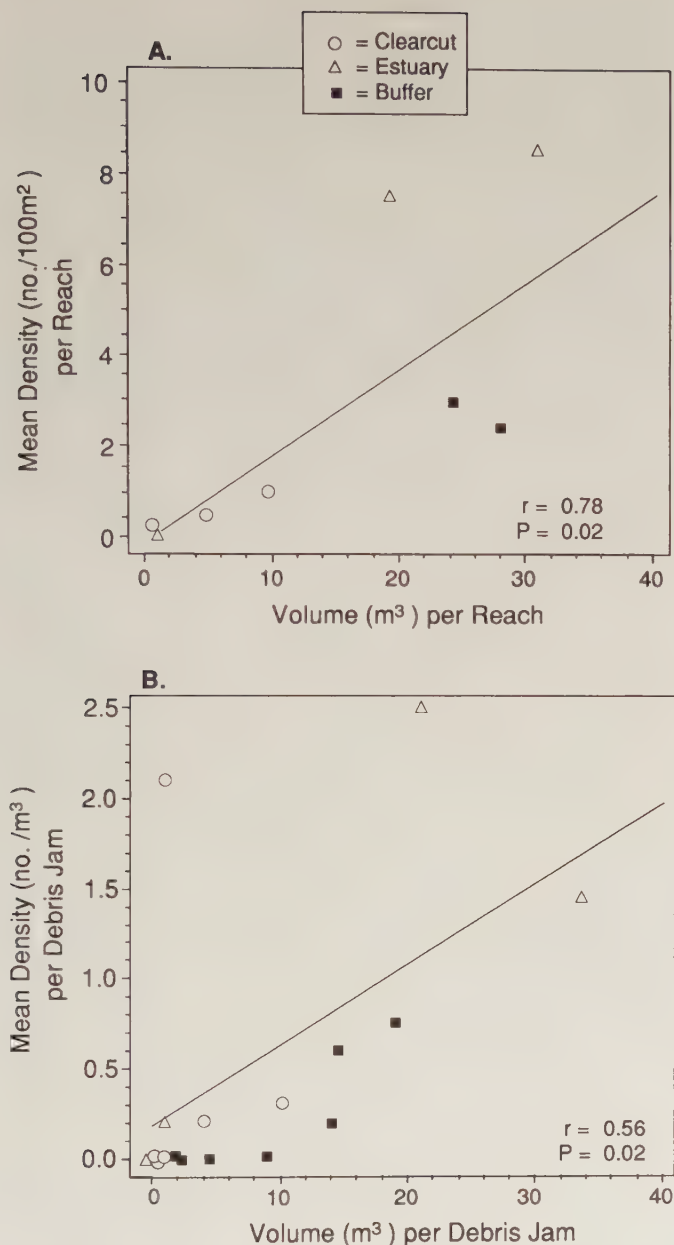


FIG. 3. Relationship between mean smolt density (no./100 m² or no./m³) and (A) volume of large woody debris per reach and (B) volume per debris jam. Location of site indicated by clearcut, buffer, or estuary symbol.

capacity for smolts in clearcut reaches of Carnation Creek, where debris volume and smolt abundance were significantly lower than in reaches bordered by a buffer strip of trees; Tschaplinski and Hartman (1983) noted a similar difference in winter carrying capacity for coho in these same sections. A notable difference between habitat use by overwintering parr and smolts was the high utilization of debris in the estuary by smolts whereas parr were absent from debris in the estuary in late winter (Fig. 2). In Carnation Creek, parr leave the estuary and return upstream in the fall with the onset of cooler temperatures and higher flows (T. G. Brown, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, unpubl. data; see also Cunjak et al. 1989).

Our observations support previous experimental studies showing that woody debris creates the preferred habitat features of slow current velocities and low light intensity (McMahon

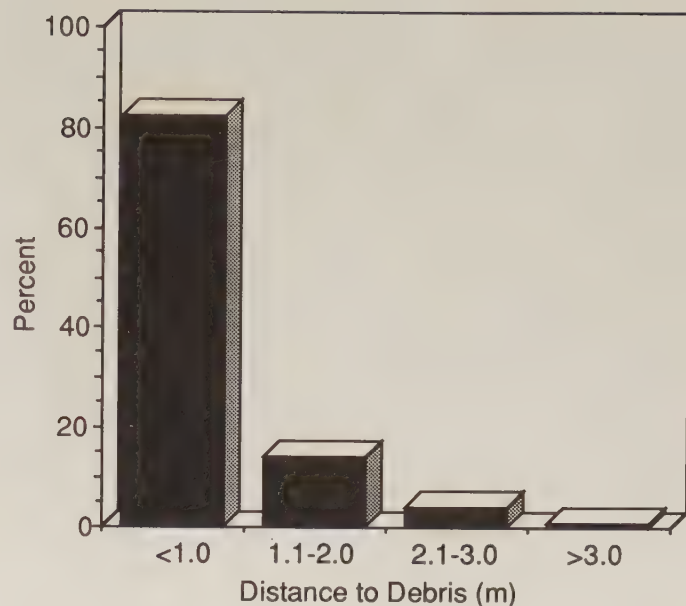


FIG. 4. Proximity of coho salmon smolts to large woody debris; $n = 1260$.

TABLE 3. Size of aggregations of coho salmon smolts observed during the first (March 30 – May 3) and second half (May 4 – June 2) of the smolt run and in the estuary relative to upstream sites (buffered and clearcut sections combined). n_a = number of aggregations observed; SE = standard error; * $P < 0.05$.

	Mean aggregation size ($\pm$ SE)	n_a
Smolt run		
First half	22.8 ± 4.5	24
Second half	$50.8 \pm 12.1^*$	13
Location		
Upstream	10.6 ± 1.8	13
Estuary	$54.5 \pm 12.6^*$	12

and Hartman 1989; Shirvell 1990). As in winter, association with these cover features likely provides smolts with shelter from high current velocities and protection from predation. Shelter from high velocity during spring freshets (Hartman et al. 1982) and tidal flushing (Macdonald et al. 1987) is likely important to prevent premature displacement into the ocean prior to completion of smoltification, especially since smolts exhibit reduced swimming abilities (Flagg and Smith 1981). Predation risk from piscivorous birds and fishes appears particularly significant for seaward migrating smolts (Elson 1962; Larsson 1985; Wood 1987). Merganser broods were frequently seen feeding in Carnation Creek and we observed several freshly scarred smolts during underwater counts in the estuary.

The results clearly show that smolts utilize the estuary as a temporary rearing environment prior to ocean entry. The 2-mo (April–May) estuarine residency period for the smolt population migrating from Carnation Creek was similar to that observed in an Oregon estuary (Myers and Horton 1982). Although individual residence times were not determined in our study, even relatively short periods of residency could enhance survival of smolts. In Carnation Creek, 50% of smolts enter

the estuary prior to completion of smoltification (McMahon and Hartman 1988). Exposure to brackish water promotes development of salinity tolerance in salmonids (McCormick et al. 1985; Tschaplinski 1988) and complete physiological adjustment of coho smolts to salinities of 25–30 ppt may require at least 36–40 h (Conte et al. 1966; Miles and Smith 1968). Estuaries may also provide enhanced feeding opportunities (Macdonald et al. 1987). Tschaplinski (1988) reported six times greater numbers of benthic invertebrates in the Carnation Creek estuary compared with upstream. Murphy et al. (1988) observed rapid growth (1.6 mm/d) for coho smolts temporarily rearing in a small Alaska estuary. Rapid growth of smolts may decrease the window of availability to nearshore predators, a major source of ocean mortality for coho salmon (Holtby et al. 1990).

Distribution and movement of smolts in the estuary are likely related to seawater affinity and osmoregulatory ability. During smoltification, coho salmon show a marked preference for seawater (Baggerman 1960; McInerney 1964). The outmigration of smolts coincident with spring tides is consistent with McInerney's (1964) contention that salinity acts as a migratory orientation mechanism for smolts. The increase in use of the lower estuary during the latter part of the smolt run may reflect increased seawater tolerance of migrants. Rodgers et al. (1987) found that downstream migrants showed increased gill (Na + K)-ATPase activity (a measure of osmoregulatory ability) over the course of the smolt migration. McMahon and Hartman (1988) noted that the silvering index, another correlate of seawater tolerance, increased in smolts entering the Carnation Creek estuary as the run progressed.

The results of our study underscore previous research on the importance of large woody debris as a structural element of coho salmon habitat. The multiple functions of woody debris in streams have been well documented (e.g. Bisson et al. 1987); however, relatively little research has addressed its role as fish habitat in estuaries. Our findings show that debris functions as cover habitat for coho salmon during smoltification and seaward migration. In the Carnation Creek estuary, deep pools with debris also serve as holding areas for returning coho and chum salmon and steelhead trout (*O. mykiss*) adults prior to their movement upstream during freshets (T. E. McMahon, pers. observ.). As in streams, debris in many Pacific Northwest estuaries has been reduced through a long history of removal (Gonor et al. 1988) and reduction in source (Bisson et al. 1987). Management practices along streams now address the need for long-term maintenance of large debris by leaving buffer strips of conifers along streambanks during adjacent timber harvest (e.g. Oregon Forest Practice Rules 1988; Bilby and Wasserman 1989); by contrast, conifer buffer strips along estuaries are currently not required in some parts of the Northwest (e.g. Oregon Forest Practice Rules 1988). Our results suggest the need to retain and manage large woody debris for salmonid habitat in estuaries as well as in streams.

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Spatial and Temporal Overlap of the American Lobster (*Homarus americanus*) and Sea Scallop (*Placopecten magellanicus*) as Related to the Impact of Inshore Scallop Dragging

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Roddick, D. L., and R. J. Miller. 1992. Spatial and temporal overlap of the American lobster (*Homarus americanus*) and sea scallop (*Placopecten magellanicus*) as related to the impact of inshore scallop dragging. Can. J. Fish. Aquat. Sci. 49: 1486–1492.

Assessment of the damage of one fishery by another requires knowledge of the overlap, in time and space, of the damaging fishing effort and the abundance of the damaged species, as well as a measure of the rate of damage. This approach was used to measure the impact of inshore scallop dragging on lobsters in Nova Scotia. Areas of reported co-occurrence of lobster and scallop grounds were surveyed by divers to determine the extent of overlap. Only 2 of 52 sites surveyed had lobsters on scallop grounds that could be dragged. Divers surveyed one site six times during 1987 and 1988 and found lobsters most abundant during August and September. Only 2% of the lobsters in the path of scallop drags were either captured or injured. The estimated value of lobsters destroyed by dragging for scallops during periods of peak lobster abundance was minor: \$757 at one site and \$176 at the other. Restricting dragging to periods of low lobster abundance significantly reduces this cost.

L'évaluation des dommages causés à une pêche par une autre pêche suppose de connaître le recouvrement, dans le temps et l'espace, de l'effort de pêche à l'origine des dommages, l'abondance de l'espèce subissant l'effet nuisible et l'importance des dommages. Cette approche a été utilisée pour mesurer l'incidence de la pêche côtière des pétoncles à la drague sur le homard en Nouvelle-Écosse. Les zones pour lesquelles on avait signalé la présence de homards sur des fonds à pétoncles ont été visitées par des plongeurs afin de déterminer l'importance du recouvrement. Seulement 2 des 52 lieux examinés présentaient des homards sur des fonds à pétoncles pouvant faire l'objet d'une pêche à la drague. Un des lieux a été examiné par plongeurs à six reprises en 1987 et 1988 et les homards se sont avérés être les plus abondants au cours des mois d'août et de septembre. Seulement 2 % des homards se trouvant dans la trajectoire des dragues à pétoncles ont été capturés ou blessés. La valeur estimée des homards détruits par le dragage des pétoncles pendant les périodes de pointe d'abondance du homard était faible: 757 \$ en un lieu et 176 \$ dans l'autre. La restriction du dragage aux périodes de faibles abondance du homard donne lieu à une baisse appréciable de ces coûts.

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Lobster fishermen in eastern Canada often complain that towed fishing gear kills or damages American lobsters (*Homarus americanus*). Several investigations have addressed specific complaints. Scarratt (1973) found that drag raking for Irish moss (*Chondrus crispus*) in northern Prince Edward Island destroyed lobsters valued at about 7% of the annual catch. Pringle and Jones (1980) and Pringle and Sharp (1980), working in western Prince Edward Island, noted that most lobsters avoided the drag rakes and that damage to lobsters was low.

Studies of possible damage by scallop gear have shown only minor overlap of sea scallop (*Placopecten magellanicus*) and lobster habitats. In 30 h of commercial scallop dragging in central Northumberland Strait, only one lobster was taken (Pringle and Jones 1980). During experimental tows in western Northumberland Strait, divers observed that in areas with subcommercial scallop densities, 12% of lobsters in the drag path were either captured, or injured but not captured, whereas in areas with commercial scallop densities, only 1% were captured or injured (Jamieson and Campbell 1985). We surmise the difference was attributable to a difference in substrates between the two areas. The fraction of the captured lobsters that were injured was not included. In another diving study, Scarratt

(1975) noted that patches of scallop and lobster habitat were usually small enough so that both were traversed by a single tow of a scallop drag, although only 12 lobsters were hit during 40 tows. In St. Marys Bay, western Nova Scotia, scallop grounds overlapped 7% of the area fished for lobsters, and these areas probably had low lobster densities (Robichaud et al. 1987).

Canadian fisheries managers have received numerous time- and site-specific requests to study the impact of towed fishing gear, especially scallop drags, on lobster stocks. The purpose of this study was to address the question of what, if any, damage to lobster populations is the result of inshore scallop fishing. Divers surveyed 51 sites of potential conflict chosen on the advice of fisheries protection officers, fishermen, and divers (Fig. 1). Another area, Port L'Hebert, was surveyed in each of 6 mo to record seasonal changes in lobster density. Data on rates of lobster encounter, capture, and injury were obtained from observations of scallop drags made by divers at this site.

Methods

Diving Surveys

Divers surveyed 51 sites on the Atlantic coast of Nova Scotia. Sites were chosen by asking fisheries protection officers in 20

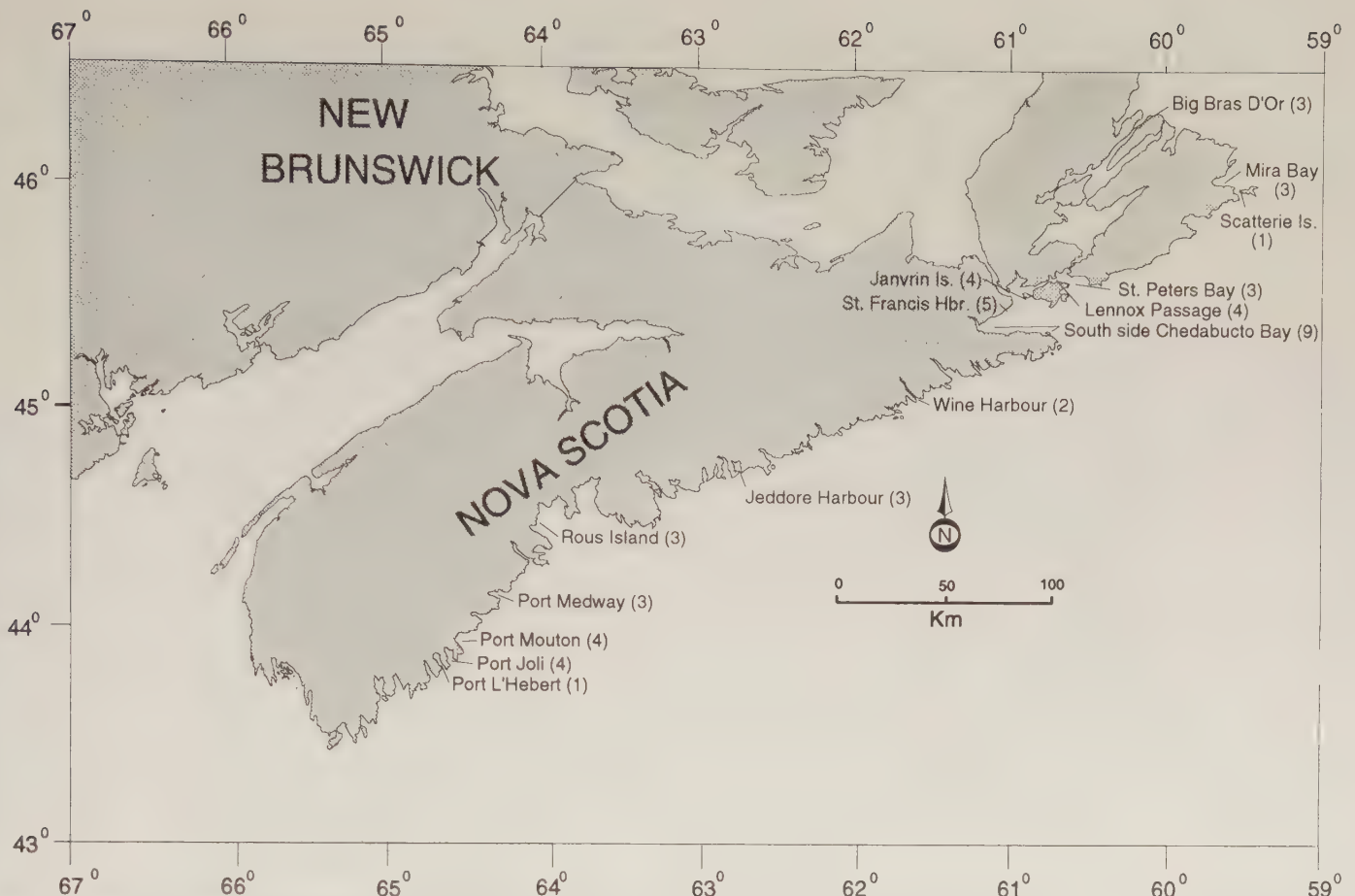


FIG. 1. Areas of reported co-occurrence of scallops and lobsters along the south coast of Nova Scotia and number of sites surveyed in each area.

regional offices to identify locations where lobster fishermen had complained of scallop fishing on lobster grounds. Also, during the surveys, local fishermen and SCUBA divers were asked to identify any additional areas where they believed lobster and scallop co-occurred. The survey was conducted during August 1989, as lobsters were most likely to be active and in open areas during August–September just after the molting season. Divers classified an area as one of potential conflict if the bottom was smooth enough to be fished by scallop drags, scallop density was >1 per 50 m^2 , and lobsters were present. A scallop density of 1 per 50 m^2 is less than commercial concentration; however, inshore scallop landings along the Atlantic coast of Nova Scotia were well below average (Department of Fisheries and Oceans, Statistics Branch). By contrast, recent lobster landings in the survey area were the highest in decades. These criteria would identify fishable lobster grounds and areas with actual or potential commercial scallop densities. If these criteria were fulfilled, three disposable 100-m transect lines were deployed, and divers counted all scallops $>40\text{ mm}$ shell height and all lobsters $>50\text{ mm}$ carapace length (CL) within 1 m on both sides of the lines. Both minimum sizes were far below commercial sizes, yet were easy for divers to see. Also, small lobsters tend not to venture out onto open bottom (Cooper and Uzmahn 1980).

Prior to the diving survey, Port L'Hebert was selected as the site for the monthly lobster sampling, as it was known from other studies to meet the selection criteria. It had a dense scallop population until recent depletion by fishing and had a dense lobster population at the time of the study (G. Sharp,

Department of Fisheries and Oceans, pers. comm.). The lobster population was surveyed by divers in September and November 1987 and in June, July, August, and October 1988 between the 16th and 25th of each month. Because the pattern of monthly abundance was consistent in both years, the data for years were combined. The study site was sheltered from ocean waves and occupied the full 60-m width of a channel. It was 360 m long in 1987 and was expanded to 450 m in 1988. Depths ranged from 7 to 11 m at low tide. Tidal amplitude was about 2 m, and tidal currents were strong, up to 100 cm/s at the surface and 60 cm/s on the bottom. The bottom cover was 70% gravel, 15% sand, and 15% boulders with no macroalgae.

For the diver surveys, four weighted baselines were permanently positioned across the channel 90 m apart. These were 60 m long and numbered continuously at 5-m intervals (i.e. $4 \times 12 = 48$ marks). Starting at a randomly chosen 5-m mark, a diver laid a 90-m-long string by drifting down current. Two divers then captured all lobsters $>50\text{ mm}$ CL located within an area 1 m on either side of the string. The divers sexed, measured, and then released the lobsters. The number of transects varied between sampling periods.

During August and October 1989, divers observed scallop drags being towed in Port L'Hebert in order to obtain data on lobster catch, avoidance, and injury. Two Digby tumbler drags, each 75 cm wide, were attached to a steel bar (Fig. 2) and towed at 0.6–1.2 m/s by a 10-m fishing boat. Inshore fishermen on the Atlantic coast of Nova Scotia use from one to four drags. For half the tows, tickler chains were fitted on the tow line in front of the drags to determine if they would induce a lobster



FIG. 2. Inshore scallop drags and tickler chain arrangement used in this study.

escape reaction and thereby reduce the bycatch. The chains were light enough so as not to damage lobsters they passed over. The number of lobsters in the path of the drags was recorded by a diver riding a tow board positioned slightly above and behind the drags and attached to the boat by a separate line. The diver also dropped a series of markers behind the drags to mark the tow path. The path was surveyed by two divers within a few minutes after each tow and all lobsters on or near the path were checked for injury.

Data Analysis

Tows with and without tickler chains were comparable. Kolmogorov–Smirnov two-sample tests showed no difference in either towing speed, tow distance, or number of lobsters encountered. This test measures the discrepancy between two cumulative distribution functions. The same test was then used to compare the number of scallops and lobsters caught and the percentage of lobsters encountered which were caught.

For the diver surveys at Port L'Hebert the total number of lobsters per 180-m² transect, the percentage of small lobsters (50–80 mm CL) per transect, and the percentage of large (>80 mm CL) lobsters that were male per transect were compared among months. A Kruskal–Wallis test was chosen because the data had many outliers and this analysis is distribution free and robust to the effects of outliers. For this test, data for each transect in all months were ranked in order and then the mean ranks among months were compared. For the two tests using percentages, transects with no lobsters or no large lobsters were omitted from the analysis rather than assigning them arbitrary values. If the test was significant, pairs of months were compared using the multiple comparison procedure and tables in Conover (1980). Because all three analyses were performed on the same data set, the critical value was set at $0.05/3 = 0.017$ to keep the probability of a type I error at <0.05. The SYSTAT package (Wilkinson 1989) was used for most of the data analysis.

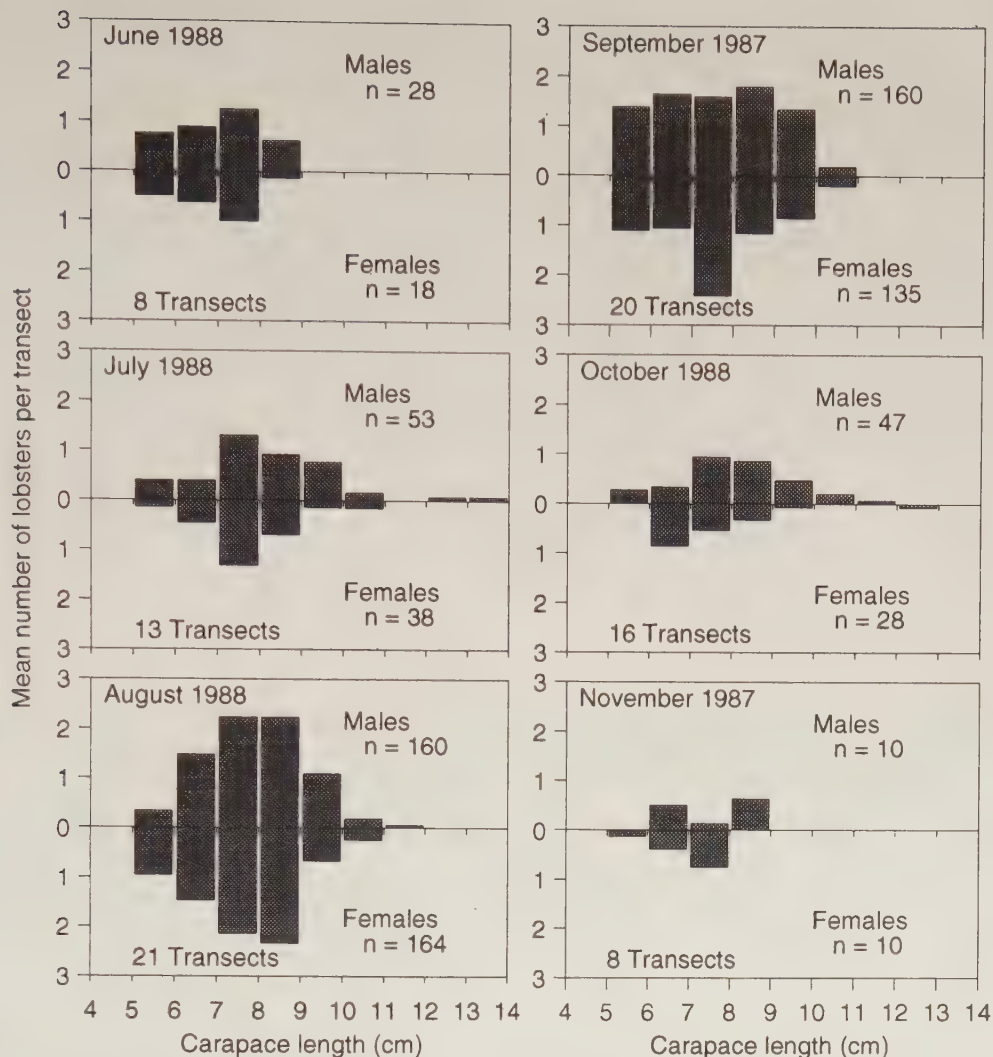


FIG. 3. Mean number of diver-caught lobsters per transect by carapace length and sex for each monthly sampling period in Port L'Hebert.

Results

Of the 51 locations surveyed by divers in August 1989, lobsters and scallops co-occurred on draggable bottom at only one. Of the remainder, 25 had scallops only, four had lobsters only, and 17 had neither. Four sites had both, but either the bottom was undruggable or scallops were very rare. The one area with both, Big Bras D'Or in eastern Nova Scotia, was a channel with high current flow, gravel bottom, and scattered boulders, very similar to Port L'Hebert. This site was surveyed twice; nine lobsters were found on 600 m² in late August 1989 and one lobster on 600 m² in late October 1990. These relative densities agreed with the seasonal differences found in Port L'Hebert.

Lobsters were most abundant in Port L'Hebert in late summer, peaking in August–September (Table 1; Fig. 3). Although the numbers of both small (50–80 mm CL) and large lobsters (>80 mm CL) peaked at the same time, the peak was more pronounced for the larger lobsters (Table 2; Fig. 3). The percentage of males did not significantly differ from 50% for any month for the smaller lobsters ($P = 0.35$). For larger lobsters, males exceeded females in every month except August, when sexes were equal (Table 3; Fig. 3). These results suggest that large females move into the site later and out earlier in the year

than large males and that the small lobsters have a longer residence time than the large ones. The peak abundance correlates well with the seasonal high temperatures of late summer. Bottom temperatures averaged 11, 9, 16, 16, 9, and 7°C during the sampling days of June, July, August, September, October, and November, respectively.

Most lobsters avoided the scallop drags by “tailflipping” away well in advance. A few, however, took an aggressive stance, turning to face the drags with their claws raised. These would eventually try to tailflip away, but sometimes either waited until it was too late to avoid capture or, in attempting to go above the drags, would hit the underside of the towing bridle and bounce back into the drag path.

The scallop drags encountered a large number of lobsters in their path (Table 4), but of these, only 2% were captured. Neither the lobster nor scallop catch differed between tows with and without tickler chains (Kolmogorov–Smirnov two-sample test). Of the 11 lobsters caught in the drags, one was uninjured, seven had minor damage, two sustained injuries that might have been fatal, and one was dead. No lobsters with recent injuries were found by the divers in the paths behind the drags. Therefore, only 3 of 664 lobsters in the drag path were likely to have been severely injured by the scallop drags.

The damage to lobsters caused by scallop dragging can now be assigned a value. The peak lobster abundance in Port L'He-

TABLE 1. Kruskal–Wallis one-way analysis of variance comparing the total number of diver-caught lobsters (>50 mm CL) per transect for each monthly sampling period in Port L'Hebert. **Significant at 0.05/3 level.

Month	No. of transects	Median no. of lobsters/transect	Mean rank
June	8	5.0	31
July	13	5.0	35
Aug.	21	13.0	59
Sept.	20	13.5	61
Oct.	16	3.5	27
Nov.	8	3.5	17
Total	86		

Kruskal–Wallis test statistic, $T = 38.96$, $df = 5$, $P = 0.000$.

Matrix of pairwise comparisons					
	June	July	Aug.	Sept.	Oct.
July	—				
Aug.	**	**			
Sept.	**	**	—		
Oct.	—	—	**	**	
Nov.	—	—	**	**	—

TABLE 2. Kruskal–Wallis one-way analysis of variance comparing the percentage of small (50–80 mm CL) diver-caught lobsters per transect for each monthly sampling period in Port L'Hebert. **Significant at 0.05/3 level.

Month	No. of transects	Median % of small lobsters/transect	Mean rank
June	7	85.7	67.7
July	13	57.1	32.5
Aug.	21	59.0	34.7
Sept.	20	61.3	40.5
Oct.	15	60.0	42.0
Nov.	6	75.0	56.6
Total	82		

Kruskal–Wallis test statistic, $T = 14.598$, $df = 5$, $P = 0.012$.

Matrix of pairwise comparisons					
	June	July	Aug.	Sept.	Oct.
July	**				
Aug.	**	—			
Sept.	**	—	—		
Oct.	**	—	—	—	
Nov.	—	—	—	—	—

bert was 15 per transect; using two drags, a commercial scallop tow would cover about 10 times the area of a transect; an inshore boat would make about 30 tows per day, and the fishable area in Port L'Hebert could be thoroughly fished over in 10 boat days.

\$756 (value of lobsters destroyed)
 = 15 lobsters/transect
 × 10 transects/commercial tow
 × 0.02 captured × 0.3 injured
 × 0.4 kg/lobster × \$7/kg
 × 30 tows/boat day × 10 boat days.

Approximately 1% of the lobster stock would be damaged if the entire area were towed over twice. This amount of fishing

TABLE 3. Kruskal–Wallis one-way analysis of variance comparing the percentage of males among large (≥ 80 mm CL) diver-caught lobsters per transect for each monthly sampling period in Port L'Hebert. **Significant at 0.05/3 level.

Month	No. of transects	Median % of large males/transect	Mean rank
June	4	100.0	55.1
July	11	66.7	41.6
Aug.	21	50.0	24.7
Sept.	20	55.1	32.9
Oct.	11	100.0	42.0
Nov.	4	100.0	60.0
Total	71		

Kruskal–Wallis test statistic, $T = 18.058$, $df = 5$, $P = 0.003$.

Matrix of pairwise comparisons					
	June	July	Aug.	Sept.	Oct.
July	—				
Aug.	**	**			
Sept.	—	—	—		
Oct.	—	—	**	—	
Nov.	—	—	**	**	—

effort would be sufficient to deplete a high scallop density. At lower initial densities the total effort and thus the value of lobsters destroyed would be lower. The value of lobsters damaged is probably too small to be of concern, but even this would be reduced to <\$95 if scallop fishing were confined to November through June. The peak lobster biomass in Port L'Hebert, at about 30 g/m², is extraordinarily high. A high commercial biomass is 10 g/m² (Miller 1985). If the same fraction of lobsters were captured and damaged in Big Bras D'Or as in Port L'Hebert, the same fishing effort in an equal area would damage \$176 worth of lobsters in August. The impact of scallop fishing in other surveyed areas would likely be nil, since scallops and lobsters did not co-occur.

Discussion

The ability to predict the damage caused by one fishery on another is a valuable tool in fisheries management. In cases of gear conflicts, a cost-benefit analysis can be used to achieve the maximum benefits from the conflicting fisheries. Accurate damage prediction requires knowledge of the overlap of the damaging effort and the species damaged and a measure of damage rate. It must also be known if there are any spatial and temporal changes in the overlap.

In inshore areas, lobsters seem most vulnerable to mobile gear in summer. Lobster abundance peaked in Port L'Hebert in August–September. This peak was slightly more pronounced for large lobsters than for small and for large females than large males. The Big Bras D'Or site also had far more lobsters in August than in late October. Near Prince Edward Island, where coastal waters warm earlier in the year than in coastal Nova Scotia, divers saw more lobsters on scallop grounds in July than May (Jamieson and Campbell 1985). On Irish moss beds in Prince Edward Island, lobster density increased from June to August (Scarratt 1973; Pringle and Sharp 1980). This seasonality means that the extent of damage will vary throughout the year, both in the quantity of lobsters destroyed and the impact on future reproduction and recruitment to the fishery.

This study showed that on the Atlantic coast of Nova Scotia, lobsters and scallops co-occurred on only 2 of 52 sites. Both

TABLE 4. Lobster and scallop catch in scallop drags in Port L'Hebert, and the results of Kolmogorov-Smirnov two-sample tests comparing tows with and without tickler chains.

Date (d/mo/yr)	Speed (m/s)	Metres towed	Setup ^a	No. of lobsters in path	No. of scallops caught	No. of lobsters caught	% lobsters caught
29/8/89	0.7	389	s	32	9	0	0
29/8/89	1.0	370	s	32	18	0	0
29/8/89	1.2	426	s	42	13	0	0
6/9/89	0.9	500	s	25	8	1	4
6/9/89	1.0	432	s	10	2	1	10
6/9/89	1.0	370	s	25	3	0	0
6/9/89	1.0	432	s	61	20	0	0
6/9/89	1.0	494	s	50	8	3	6
29/8/89	1.2	355	t	30	7	2	7
29/8/89	1.2	444	t	34	28	0	0
30/8/89	0.8	139	t	30	9	0	0
6/9/89	1.0	556	t	34	7	0	0
6/9/89	1.0	494	t	68	6	2	3
6/9/89	1.0	556	t	49	10	0	0
6/9/89	1.0	494	t	56	5	1	2
6/9/89	1.0	494	t	86	10	1	1
Means, all tows	1.0	434		41.5	10.2	0.69	2
Means, standard	1.0	427		34.6	10.1	0.63	3
Means, ticklers	1.0	441		48.4	10.3	0.75	2

Kolmogorov-Smirnov two-sample tests, tickler versus standard setup

Variable	Max. difference	Two-sided probability
Speed	0.125	1.000
Meters towed	0.500	0.188
Lobsters encountered	0.375	0.520
% lobsters caught	0.250	0.906
No. of lobsters caught	0.125	1.000
No. of scallops caught	0.250	0.906

^as = standard; t = with tickler chains.

sites were characterized by sheltered channels with fast currents and gravel bottom. In St. Marys Bay, one of six sites investigated by divers had both scallops and lobsters, but the lobsters were in low abundance (Robichaud et al. 1987). This area also had fast currents but the bottom was composed of mud among boulders. In an area of patchy habitat in Northumberland Strait, half of the locations had both scallops and lobsters, although the lobsters were in low abundance (Scarratt 1975). Areas with abundant scallops had no lobsters.

The addition of tickler chains to the scallop drags does not appear to reduce their impact on lobsters. The lack of difference in percentage of lobsters caught with and without ticklers can be explained by the divers' observation that the tickler chains did not prompt an escape reaction. Most lobsters that took an aggressive stance (claws raised) retained this posture as the tickler chains passed over.

Two factors not examined directly in this study are the impact of scallop dragging on lobsters <50 mm CL and on lobster habitat. Lobsters <50 mm CL were rarely observed out of shelters, and they were not observed in the drag tracks; Jamieson and Campbell (1985) showed that they pass undamaged through the rings making up the body of the scallop drags. The impact on lobster habitat is difficult to quantify. However, the most intensive inshore scallop fishery in Nova Scotia is near Digby and the oldest is in Mahone Bay, Lunenburg County. Both of these areas have recently reported the highest lobster landings that have occurred during the >70-yr history of the

scallop fishery. Thus we have evidence against both injury to small lobsters and negative impact on lobster habitat.

The value of lobsters destroyed by scallop drags or Irish moss rakes is generally considered to be low. In a season's fishing of a scallop bed in Northumberland Strait, an estimated \$73 worth of lobsters were destroyed in the process of catching \$12 483 worth of scallops (Jamieson and Campbell 1985). Scarratt (1973) estimated that the value of lobsters destroyed by Irish moss raking in northern Prince Edward Island was 18% of the total value of the Irish moss landings and 7% of the value of the lobster landings. For western Prince Edward Island, Pringle and Sharp (1980) estimated that Irish moss rakes injured 1.3–2.7% as many lobsters as the lobster fishery caught. Fishing effort sufficient to remove a commercial density of scallops in Port L'Hebert would damage only 1% of the lobster stock. This would be valued at \$756 during peak lobster abundance and far less during other times. The peak value for equivalent fishing effort and area in Big Bras D'Or would be \$176. The high catch rates of lobsters by otter trawls (Robichaud et al. 1987; Simon and Campana 1987; Smith and Howell 1987) make this gear a greater threat to lobster stocks.

The study was carried out at a time when the lobster landings, and presumably lobster abundance, were near historic highs for both the Port L'Hebert and Big Bras D'Or areas; thus the estimated damage to the lobster fishery would also be near the long-term maximum. This study shows that the extent of possible damage to lobsters by nearshore scallop fishing is mini-

mal. In most areas the two do not co-occur; in the few areas where they do co-occur, it is on a seasonal basis; thus, area closures during peak abundance could minimize the damage.

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Spatial Heterogeneity of Littoral Fish Assemblages in Lakes: Relation to Species Diversity and Habitat Structure

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Benson, B. J., and J. J. Magnuson. 1992. Spatial heterogeneity of littoral fish assemblages in lakes: relation to species diversity and habitat structure. *Can. J. Fish. Aquat. Sci.* 49: 1493–1500.

We quantified the spatial heterogeneity in nearshore fish community composition within six Wisconsin lakes and examined its relation to habitat heterogeneity and species diversity. Fish abundance was estimated annually (1981–84) using seines at six sites in each lake. Substrate type, macrophyte growth form, and depth gradient were noted at each site. Species richness was estimated as the expected number of species when the number of individuals was held constant over lakes (rarefaction). Fish community spatial heterogeneity (the average percent dissimilarity in fish species composition over all possible pairs of seine sites within a lake) differed among lakes; it was positively correlated with within-lake variation in the depth gradient and with species diversity as estimated by rarefaction. We tested whether differences in community spatial heterogeneity among lakes resulted simply from differences in species diversity using a randomization test based on random permutations of the rows (seine hauls) in the species composition data matrix. Lakes differed in the extent to which the observed community heterogeneity exceeded the randomization results. Spatial heterogeneity of the fish community, as opposed to sampling phenomena resulting from differences in richness, was a strong factor in some lakes.

Les auteurs ont quantifié l'hétérogénéité spatiale de la communauté de poissons fréquentant les eaux du littoral de six lacs du Wisconsin et ont examiné sa relation avec l'hétérogénéité de l'habitat et la diversité spécifique. À cette fin, l'abondance annuelle des poissons a été déterminée de 1981 à 1984 par sennage à six sites dans chaque lac. Le type de sédiment, les espèces de macrophyte et le gradient de profondeur à chaque site ont aussi été relevés. La richesse spécifique a été établie comme le nombre attendu d'espèces lorsque le nombre d'individus étaient gardés constants dans tous les lacs (raréfaction). L'hétérogénéité spatiale de la communauté ichthyenne (la différence moyenne en pourcentage entre la composition des communautés ichthyennes en fonction de toutes les paires possibles de sites de sennage dans un lac) a varié selon les lacs; elle était en corrélation positive avec la variation intralacustre du gradient de profondeur et la diversité spécifique telle qu'établie par la raréfaction. Les auteurs ont vérifié par randomisation si les différences entre l'hétérogénéité spatiale interlacustre des communautés étaient simplement le résultat de différences entre la diversité spécifique; cette randomisation était basée sur des permutations aléatoires des rangées (traits de senne) dans la matrice de données sur la composition spécifique. Le degré jusqu'à lequel l'hétérogénéité observée des communautés était supérieure aux résultats de la randomisation variait selon le lac. L'hétérogénéité spatiale de la communauté ichthyenne, par opposition aux phénomènes de l'échantillonnage issus de différences de la richesse spécifique, était un important facteur dans certains lacs.

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The patchy distribution of organisms has important consequences for community structure and dynamics. Spatial heterogeneity can mediate competitive or predatory interactions (Huffaker 1958; Magnuson 1962; Kaiser 1983; Gilinsky 1984; Holt 1984) and enable otherwise incompatible species to coexist or modify intraspecific behavior. Patchiness in the distribution of organisms can influence the intensity of ecological disturbances and how frequently they occur (Sousa 1984). To understand the role of spatial heterogeneity in the functioning of natural communities, it is necessary to quantify that heterogeneity and relate it to other determinants of community structure.

We examined how the within-lake spatial heterogeneity in nearshore fish communities varied over time and how it was related to lake morphometry, fish habitat structure, and fish species diversity. Lakes with physically more complex environments may have more diverse fish habitat as represented here by such measures as variation in substrates, macrophytes, and depth gradients. These habitat factors may affect the diversity of prey, spawning sites, or cover and thus influence fish

community responses such as species richness and community spatial heterogeneity.

We quantified the variability in fish species composition among multiple sites within each lake using a community heterogeneity index (CHI) which is a measure of beta diversity. The usual definition of beta diversity refers to the rate of change in species composition along an environmental gradient (Whittaker 1972; Pielou 1975; McNaughton and Wolf 1979). However, the concept of beta diversity has not been restricted to coenoclines but has also been applied to diversity between habitats (Ter Braak 1983). Beta diversity is intended to be the component of diversity due to habitat changes across sites (Cody 1975). In addition to the component of spatial variation due to habitat heterogeneity and associated species preferences, CHI contains variation due to within-species social behavior such as schooling or territoriality.

We focus on the relation of CHI with habitat heterogeneity. Many fishes segregate by habitat along gradients of distance from shore, vegetation structure, temperature structure, and depth in the water column (e.g. Werner et al. 1977; Johnson

and Stein 1979; Brandt et al. 1980; Crowder and Magnuson 1983; Keast 1984; Killgore et al. 1989). Structural complexity influences prey community structure (Crowder and Cooper 1982). Therefore, we expect that differences among lakes in habitat heterogeneity would lead to differences in community spatial heterogeneity.

CHI also may correlate with species diversity because (1) the size of the species pool influences sampling variability or (2) both species richness and community spatial heterogeneity are functions of habitat heterogeneity. Species diversity is positively related to habitat heterogeneity in several assemblages, both terrestrial (MacArthur and MacArthur 1961; Pianka 1967) and aquatic (Abele 1974; Bronmark 1985). More specifically, fish species diversity is associated with lake area (Barbour and Brown 1974; Eadie et al. 1986) and with a variety of measures of habitat heterogeneity and area (Tonn and Magnuson 1982; Eadie and Keast 1984).

In this paper we examine how the spatial heterogeneity in nearshore fish communities varied over time and among lakes, and we test the hypothesis that community spatial heterogeneity is positively influenced by habitat heterogeneity. We also hypothesize that an association between species diversity and the community spatial heterogeneity results because habitat heterogeneity also influences species richness. We test whether differences among lakes in community spatial heterogeneity could be accounted for by differences in species diversity assuming an underlying homogeneity in fish distribution within each lake.

Methods

Site Description and Field Methods

Fish communities of five lakes in northern Wisconsin (Allequash, Big Muskellunge, Crystal, Sparkling, and Trout lakes) and Lake Mendota in southern Wisconsin were sampled annually in late summer from 1981 to 1984 by the North Temperate Lakes Long Term Ecological Research Project. These lakes vary from 37 to 3986 ha and from oligotrophic to eutrophic (Table 1).

Sampling consisted of 18 seine hauls per lake (three hauls at each of six sites) per year. The shoreline of each lake was divided into 100-m segments; six segments, chosen at random in the first year, were used as sites for seining. In Mendota, seine sites were restricted to seinaable beaches after 1982. At each site, we divided the 100-m shoreline segment into thirds and usually made a seine haul in each third. Seining in a lake

was on two consecutive nights using a 12.2 × 1.2 m seine (6.4-mm stretch mesh) with a 1.2 × 1.2 × 1.2 m central bag (3.2-mm stretch mesh). Seiners walked parallel to shore with the deeper seiner at the 1-m depth contour and the net extended to an 8-m width. At approximately 25 m, the shallow seiner stopped and the deeper seiner walked in an arc until both were equidistant from the shore, and then both hauled the seine to the shore. Fish were identified to species and counted. Sampling dates ranged from late July through August for the five northern lakes and from late August to mid-September for Mendota.

In July 1986 (July 1990 for Mendota), we collected data on macrophyte growth form, substrate structure, and depth gradient to characterize the habitats at seine sites for each lake. The shoreline at each seine site was divided into thirds as described earlier for fish sampling and we walked a transect in the middle of each third from the shore to a depth of 1 m, yielding a total of 18 transects per lake. The distance from the shore to the 1-m depth was used to calculate a depth gradient. Macrophytes within 1 m of the transect were classified by growth form (rosette, flexuous, emergent, floating (Fassett 1930)). At one quarter and three quarters of the distance along the transect, we characterized the substrate as muck, sand, gravel, cobble, or some combination of these categories. The substrate category of a transect included both its nearshore and offshore station (e.g. the substrate category might be sand-gravel-cobble close to shore and sand off shore).

Statistical Methods

Community Heterogeneity Index (CHI)

The spatial variability in fish species composition was quantified for each lake in each year with CHI defined as the average percent dissimilarity over all possible pairs of seine sites within a lake (usually 15 pairs, i.e. the number of combinations of six sites taken two at a time); the percent dissimilarity between sites j and k (PD_{jk}) was defined as

$$PD_{jk} = 100 - 200 \left\{ \frac{\sum_{i=1}^n \min(a_{ij}, a_{ik})}{\sum_{i=1}^n a_{ij} + a_{ik}} \right\}$$

where a_{ij} is the abundance of species i at site j and n is the number of species (Gauch 1982). It measures the departure from homogeneous species composition among sites within a lake and ranges between 0 and 100, where 0 represents homogeneity. To estimate abundance, data from the three hauls for each site were summed and then relativized by the total number of individuals caught at each site in a given year. The

TABLE 1. Morphometric and limnological characteristics of the six Wisconsin study lakes.

	Crystal	Sparkling	North Allequash	Big Muskellunge	South Trout	Mendota
Area (ha)	37	64	112	396	1091	3986
Shoreline development index ^a	1.02	1.34	1.68	2.35	1.72	1.60
Mean depth (m) ^b	10.4	10.9	3.8	7.5	14.9	12.2
Conductivity (μS/cm) ^c	13	76	84	45	90	295.0–440.0
pH ^d	5.72	7.14	7.29	7.07	7.41	8.1
Secchi depth ^e	8.3	6.6	3.0	7.2	4.6	2.0

^aShoreline development factor = $S/[2(a\pi)^{-1/2}]$ where S = shoreline length and a = area.

^bFrom Robertson (North Temperate Lakes LTER, lake morphometric data, pers. comm.).

^c1984 summer mean (averaged over sample dates in the period June 1 through August 31) at the surface.

^dMean of all samples at spring and fall mixis (1981–83); Mendota (1980–81) (Brock 1985).

^eMean summer Secchi (averaged over sample dates in the period June 1 through August 31 in 1982–83); Mendota (1979–80).

corresponding similarity index has been called Czekanowski's Index, Bray-Curtis Index, Index of Affinity, or Proportional Similarity and was shown by Bloom (1981) to measure similarity accurately in contrast with the other indices tested.

We wanted to examine whether CHI differed among the lakes. Probable serial correlation among years makes years pseudoreplicates; therefore, a repeated measures analysis was appropriate. A sphericity test was applied to determine if the covariances were such that the usual *F*-tests are exact (SAS Institute Inc. 1988). Then, a two-way ANOVA including Tukey's one degree of freedom test for nonadditivity was performed.

CHI was determined at two additional spatial scales: within site and among lake. Because multiple seine hauls were made at almost all sites each year, within-site CHI could be estimated. The within-site CHI was calculated by averaging the percent dissimilarity among all combinations of pairs of hauls for each site and then averaging over sites for each lake. We also calculated an among-lake CHI as the dissimilarity in species composition between lakes averaged over years. Our primary scale of interest, however, was the among-site CHI defined earlier. In the remainder of the paper, CHI without a modifier refers to among-site CHI.

Contrasting these three indices for each lake represents a nested comparison at three spatial scales (among lakes, among sites within a lake, and among hauls within a site). We expected that the within-site CHI would be less than the among-site CHI which would be less than the among-lake CHI because we assumed that habitat would be more similar among seine hauls at a given site than among sites and more similar within lakes than among lakes.

Habitat Heterogeneity

We computed measures of habitat heterogeneity for macrophyte growth form, substrate structure, and depth gradient using the Shannon-Wiener diversity index (Shannon and Weaver 1949) based on 18 transects per lake. Depth gradient was transformed into a categorical variable by creating slope intervals of 0.02 m/m.

We examined the relations of the macrophyte, substrate, and depth gradient diversity with CHI. Given that a larger lake with a more complex shoreline might provide greater habitat diversity, we also tested the relations of CHI with lake area and the shoreline development index (a measure of shoreline convolution (Welch 1948)).

Rarefied Species Richness

The relation between community heterogeneity and species richness was examined using the technique of rarefaction (Hurlbert 1971; Smith and Grassle 1977) to adjust the number of species caught for differences in the number of individuals caught. The total number of fish caught per year in a lake ranged from 70 to 4888. Rarefied species richness was calculated as the expected number of species if the number of individuals caught had been 50. Rarefied species richness contains components of both richness and evenness and hence is a measure of species diversity.

Randomization Test

We considered the possibility that differences in CHI among lakes might result purely from differences in species richness among lakes even if communities were spatially homogeneous.

Differences among sites in a spatially homogeneous community would be a matter of chance or sampling variability. We reasoned that if one assumed that species composition was not related to seine site attributes, sampling phenomena alone could give rise to greater variability among samples in a more diverse community.

We performed a randomization test (Fisher 1935; Bradley 1968) to estimate the probability of obtaining values of CHI at least as extreme as observed under the hypothesis that one is sampling from the same underlying community at all sites. The null model states that species composition of an individual seine haul is assigned to sites at random and hence each permutation of the data matrix has an equal probability.

The randomization procedure generates a null distribution for CHI (Fig. 1). We randomly permuted the rows of the original data matrix where rows represented seine hauls and columns represented species. The assumption is that no relation exists between the seine catch and sites. Note that in randomizing the data matrix, we kept the seine hauls intact; thus, any species interactions which determine the composition of an individual haul are still represented in the randomized data matrix.

One thousand randomized matrices were generated for each lake-year, and simulated values of CHI were calculated from the randomized matrices. The 1000 simulated CHI's for each lake-year were used to construct a frequency distribution for CHI. The observed CHI for a lake was compared with this frequency distribution; the proportion of simulated values greater than or equal to the observed CHI is an approximate *p* value. When *p* was small rather than large, we concluded that the distribution of species among sites was heterogeneous rather than a result of sampling variability biased by differences in species diversity among lakes.

Results

Community Heterogeneity

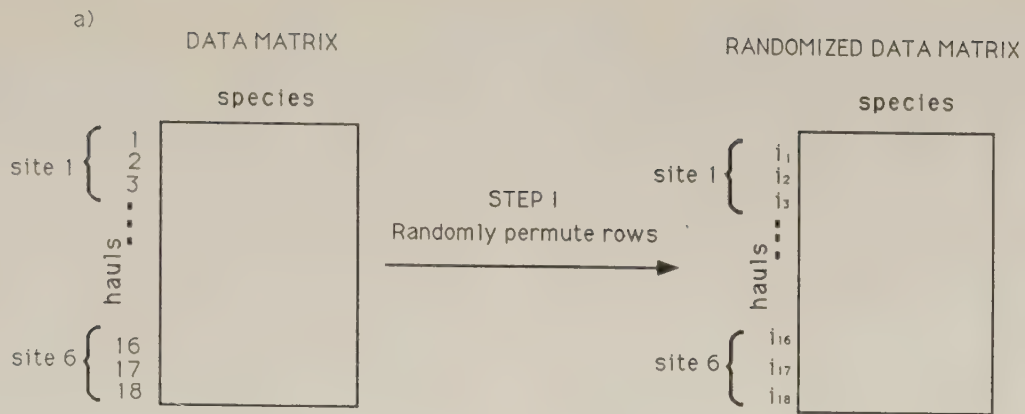
CHI for each lake was relatively constant across years (Fig. 2). The sphericity test in the repeated measures analysis ($p = 0.975$) validated the use of two-way ANOVA to test year and lake effects. Lakes were significantly different whereas years were not (Table 2). Tukey's one degree of freedom test for nonadditivity estimated that the interaction term was not significant. Lakes were ranked by average CHI (from least to most heterogeneous) as Crystal, Mendota, Sparkling, Trout, Allequash, Big Muskellunge.

Restriction to seinable beaches in Lake Mendota (1982-84) might have caused CHI to be underestimated because we were not sampling a representative collection of habitats. However, the lowest CHI occurred in 1981, the year in which the most physically diverse habitats were sampled (CHI for 1981-84 = 10.4, 13.4, 27.0, 12.4).

The among-sites CHI was similar to the among-hauls CHI (Fig. 3). Big Muskellunge was the only lake where among-site CHI's were greater than within-site CHI's for most years.

Community Heterogeneity as Related to Habitat Structure and Species Richness

The average CHI for each lake was correlated with both habitat structure and rarefied species richness (Table 3). Correlations with macrophyte diversity, depth gradient diversity, and rarefied richness were all at least 0.90. According to the Bonferroni criterion for multiple tests, however, only the correlations with depth gradient diversity and rarefied richness were



STEP II: Compute heterogeneity index = average percent dissimilarity among all pairs of sites

STEP III. Repeat Steps I and II 1000 times to generate a frequency distribution for the heterogeneity index.

STEP IV. Compare the observed value with the frequency distribution and calculate the proportion of the distribution which is as or more extreme than the observed value.

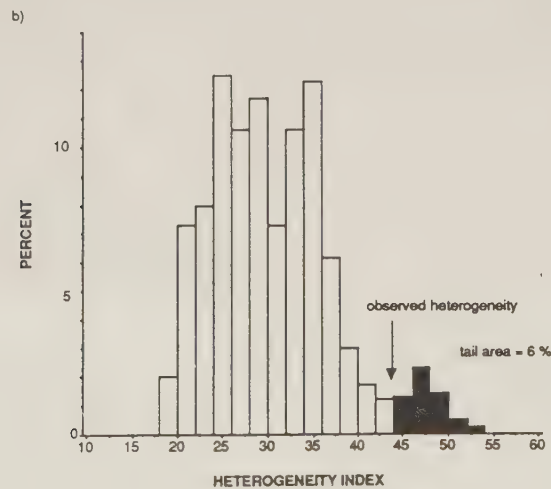


FIG. 1. (a) Schematic diagram of the randomization test procedure. (b) Example of the null distribution of the heterogeneity index generated by the randomization procedure on the data from Trout, 1981. The arrow indicates the observed value of the heterogeneity index.

significant ($p < 0.05$, Fig. 4). Using this criterion, only strong effects will be significant given our small sample size ($n = 6$).

Randomization Test

If the CHI were the result of random shuffling of seine hauls among sites, the expected proportion of simulated values greater than or equal to the observed CHI in 1000 simulations would be 0.5. The average p values estimated from the randomization test ranged from 0.03 for Big Muskellunge to 0.47 for Lake Mendota (Table 4). Except for Mendota in 1981 with 1.0, the proportion of simulated values at least as great as the observed was less than 0.5 for all lake-years (Fig. 5). For Big Muskellunge and Trout, the average p value was less than 0.05. When

p is large, the observed heterogeneity cannot be distinguished from random variation whereas a small p implies strong community heterogeneity.

Ordering the lakes by the average p value closely matches the ranking by rarefied richness (Table 4). The mean simulated CHI is positively correlated with rarefied richness ($p = 0.001$ and $n = 6$). Hence, a component of the observed differences among lakes in CHI is attributable to differences in species diversity. However, the differences between the observed CHI and the mean simulated CHI increased with the mean rarefied richness ($p = 0.01$ and $n = 6$). Thus, lakes with greatest species diversity are also those where the observed CHI most exceeds the randomized results.

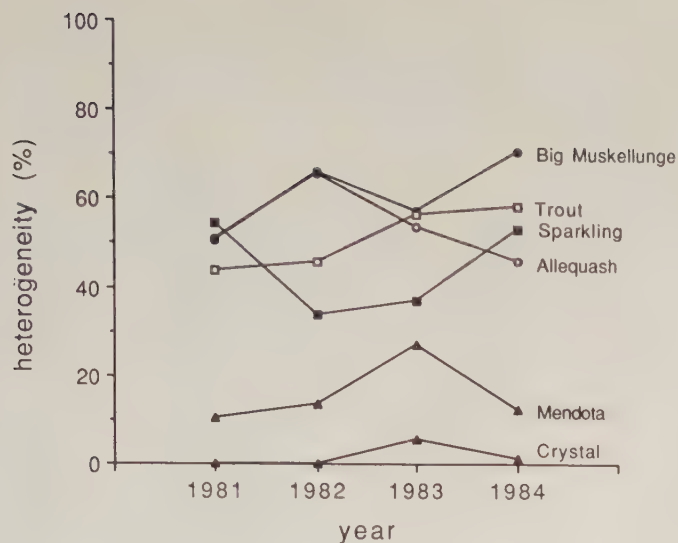


FIG. 2. Community heterogeneity for 1981–84 for six lakes.

TABLE 2. Results of repeated measures analysis including a one degree of freedom test for nonadditivity.

Source	df	SS	MS	F	p
Year	3	107.67	35.89	0.48	0.70
Lake	5	11443.68	2288.74	30.56	0.0001
Estimated interaction	1	1.28	1.28	0.02	0.90

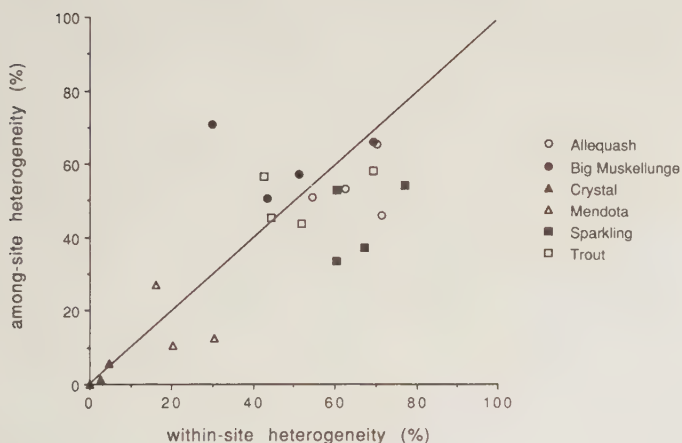


FIG. 3. Relation between the among-site heterogeneity and the within-site heterogeneity for each lake-year. The line represents the points where among-site heterogeneity equals within-site heterogeneity.

TABLE 3. Correlations between the average CHI for each lake and variables related to habitat structure and richness ($n = 6$). The community heterogeneity was averaged over years for each lake; the habitat diversity values were based on 18 transects per lake using the Shannon–Wiener diversity index.

	Correlation	p
Area	-0.35	0.492
Shoreline development index	0.75	0.085
Substrate diversity	0.81	0.0498
Macrophyte diversity	0.91	0.0117
Depth diversity	0.96	0.0028 ^a
Rarefied richness	0.98	0.0004 ^a

^aSignificant at an error rate of 0.05 (Bonferroni criterion).

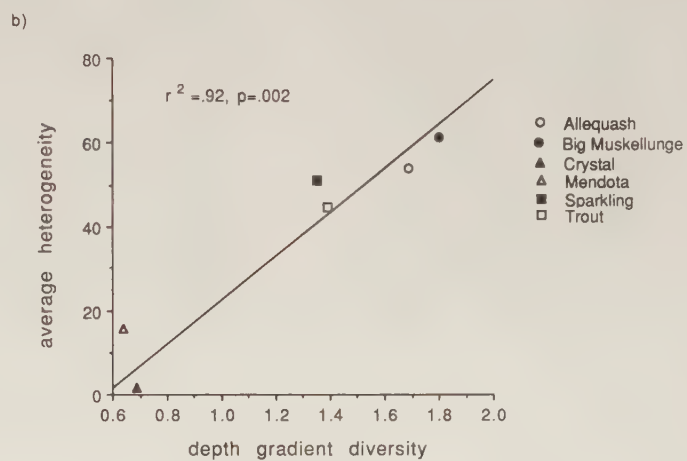
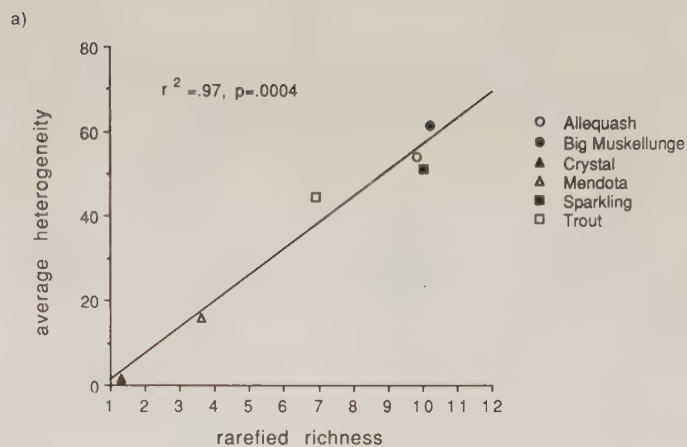


FIG. 4. (a) Relation between average (over years) community heterogeneity and average rarefied richness. (b) Relation between average (over years) community heterogeneity and depth gradient diversity.

Discussion

Community Heterogeneity Index

The among-site spatial heterogeneity of the nearshore fish in our six study lakes was relatively stable over years for each lake and differed among the lakes. Gelwick and Matthews (1990) quantified the within-lake variation in community composition across habitat types using Kendall's coefficient of concordance based on the 10 most abundant species in Lake Texoma, a reservoir, and found that the amount of concordance across habitat types changed seasonally. This represents the only other study we know that quantifies the within-lake spatial variation in fish communities.

An unexpected result in our study was that the community heterogeneity among seine hauls at a site was not generally less than that among sites. Apparently, fine-grained patchiness of organisms responding to small-scale spatial heterogeneity or social aggregation at a subsite or subhaul level is larger than we had expected. Fish can aggregate at a scale smaller than our smallest sampling unit, i.e. 33 m of shoreline. Other possible sources of within-site heterogeneity include sampling error and disturbance from the preceding seine haul. We doubt the disturbance explanation because we worked at night and because the distance between hauls onto the beach was 25 m.

The low community heterogeneity for Lake Mendota seems to result from high dominance. Lyons (1989) and Magnuson and Lathrop (1992) have documented that the diverse littoral-

TABLE 4. Proportion of simulated heterogeneity index values greater than or equal to the observed value for 1000 randomized matrices and the rank order (where rank 1 is the highest) by measures of species richness and habitat structure. Entries are omitted for years in Crystal when only one species was caught. Lakes are ordered by the mean proportion of simulated values greater than or equal to observed.

Lake	Proportion $\geq$ observed				Mean proportion	Rank			
	1981	1982	1983	1984		Rarefied richness	Substrate diversity	Macrophyte diversity	Depth diversity
Big Muskellunge	0.11	0.01	0.00	0.00	0.03	1	1	2	1
Trout	0.06	0.00	0.00	0.11	0.04	2	2	3.5	4
Allequash	0.12	0.04	0.07	0.30	0.13	3	4	1	2
Sparkling	0.12	0.30	0.44	0.09	0.24	4	5	3.5	3
Crystal	—	—	0.27	0.46	0.36	6	6	6	5
Mendota	1.00	—	0.23	0.19	0.47	5	3	5	6

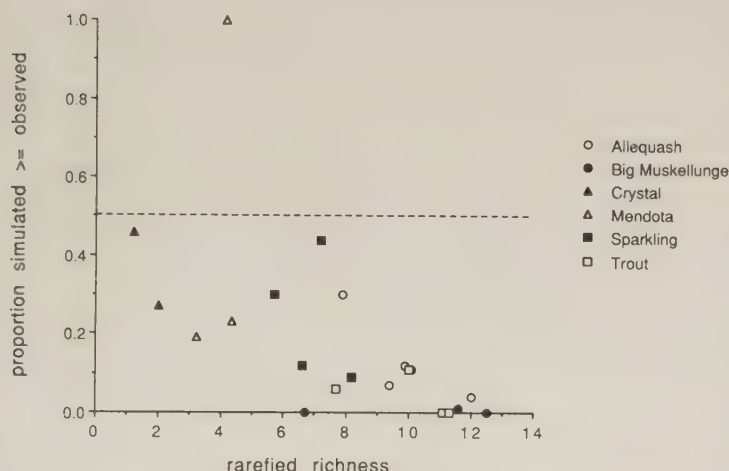


FIG. 5. Relation between the proportion of simulated heterogeneity indices for a lake-year greater than or equal to the observed heterogeneity index in 1000 randomizations of the original data matrix and rarefied richness. Points are omitted for years in Crystal when there was only one species caught. The broken line represents the expected value of this proportion under the null hypothesis.

zone assemblage of small fish species that used to be present in Lake Mendota has been replaced by an assemblage dominated by one small species and strong year classes of several intermediate and large fishes.

Role of Species Diversity and Habitat Structure

Fish species richness in many aquatic environments has been related to habitat heterogeneity (Tonn and Magnuson 1982; Eadie and Keast 1984; Rahel 1984; Sale and Douglas 1984). Our results indicate that spatial heterogeneity in community composition is related to habitat heterogeneity, especially depth gradient diversity. Greater diversity in habitats within a lake appears to create an opportunity for a more spatially heterogeneous fish community.

Several other studies have examined depth diversity as a factor related to community structure. Tonn and Magnuson (1982) found that vegetation diversity as opposed to substrate or depth diversity was significantly related to summer differences in species richness among lakes but they also noted that their selection of lakes limited the range of substrates and depths so that vegetation was the primary habitat dimension along which the lakes varied. Eadie and Keast (1984), looking at the within-lake variation, did not find a significant relation between species richness and depth diversity although they did find significant relations with other measures of habitat heterogeneity. Moyle

and Vondracek (1985) looked at a variety of habitat measures in an analysis of niche overlap in streams and found that the relative depth of the fish was one of two factors with the lowest niche overlap. Thus, the prior evidence on the importance of depth diversity in structuring fish assemblages has been mixed.

In our study, CHI was strongly correlated with species diversity, measured as rarefied richness. However, this correlation appears to derive from the relations of both community heterogeneity and species diversity to habitat heterogeneity. We rejected the hypothesis that the pattern of differences in CHI among lakes was a sampling phenomenon due to differences in species richness. Thus, spatial heterogeneity as opposed to sampling phenomena was the strong factor contributing to community heterogeneity in Big Muskellunge and Trout. In lakes with more homogeneous habitats at seine sites, Crystal and Mendota, the simulations suggested that random variation was a larger component of the CHI than in lakes with greater habitat heterogeneity.

Issues of Scale

Spatial heterogeneity in community composition and the analysis of its relation to habitat heterogeneity are scale dependent. Our sites were 100-m stretches along the shoreline; our seine hauls were 33-m stretches within these sites. Smaller scale heterogeneity (e.g. presence or absence of fallen logs, macrophyte beds, rocks) existed which could influence spatial variability in community composition. We also studied the variability in species composition at a larger scale, i.e. among the lakes (Benson, Guo-Zhang, Magnuson, and McLain, unpubl. data). The among-lakes spatial heterogeneity in species composition exceeded both the among-sites and among-hauls heterogeneity (Fig. 6). However, Crystal with essentially only one species was responsible for the greater among-lakes heterogeneity. If Crystal had not been included, among-lakes heterogeneity would have been similar to among-sites and among-hauls heterogeneity.

Tonn (1990) and Tonn et al. (1990) presented a conceptual framework for understanding the different spatial and temporal scales over which processes structuring fish assemblages have their effects. They view the structuring factors, events, and processes as a series of filters acting on the potential fish fauna at continental, regional, lake-type, and local scales to produce the local fish assemblage of a particular lake. Our study can be placed in this framework as an additional filter of within-lake factors which act on the local fish assemblage to produce the within-lake spatial distribution of fishes.

CHI measures the average dissimilarity in species composition between pairs of sites. It is possible for the species at a

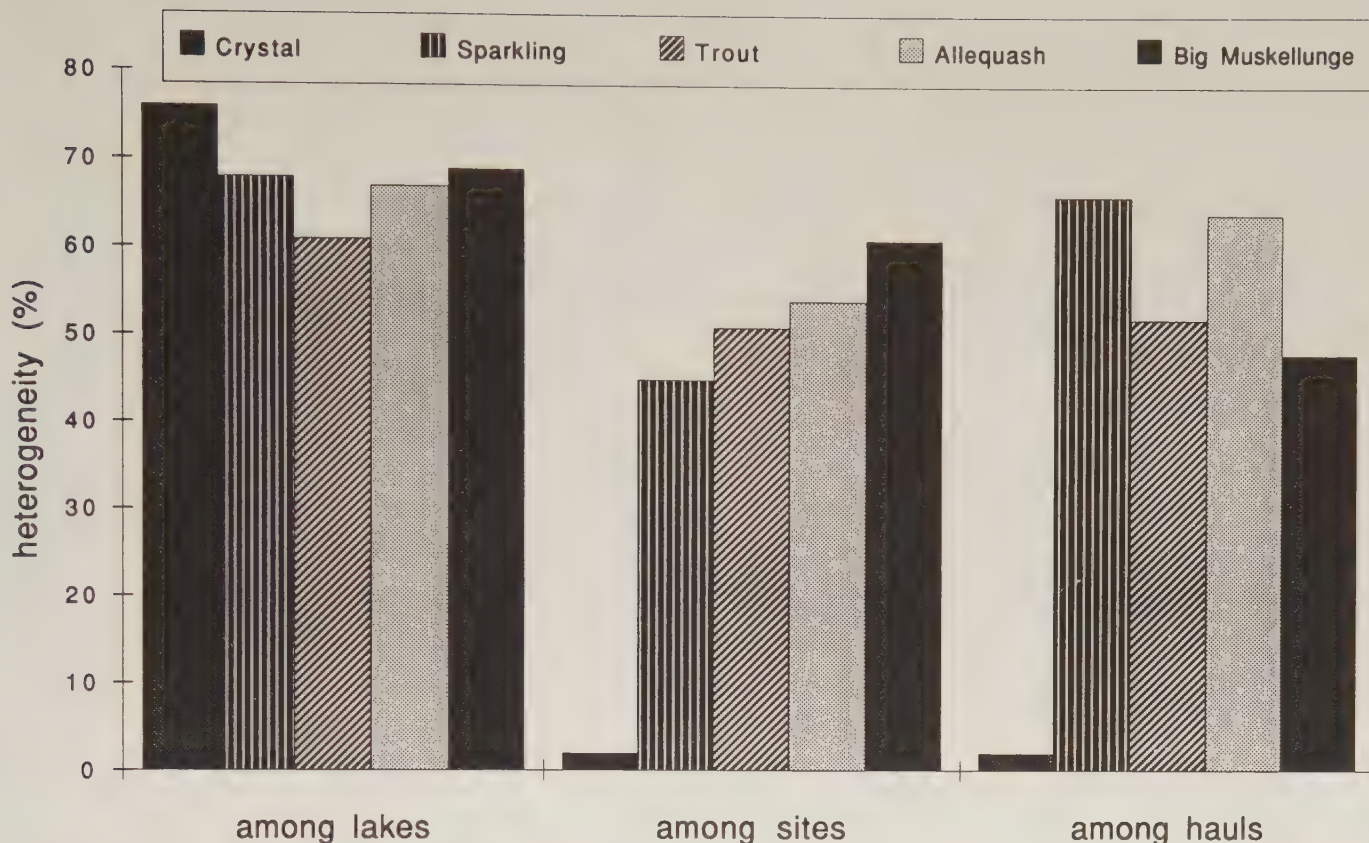


FIG. 6. Comparison of the community spatial heterogeneity at three different spatial scales: among lakes, among sites within a lake, and among hauls within a site for five lakes.

lake scale to change and the community heterogeneity within a lake to remain relatively constant. For example, the Mendota fish community switched from dominance by black crappie (*Pomoxis nigromaculatus*) in one year to dominance by brook silverside (*Labidesthes sicculus*) in another, but the change in CHI was small. Thus, CHI is a measure of community structure at a different scale than species composition of the lake per se and is potentially more sensitive to changes in habitat structure than to changes in species over time.

Acknowledgements

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Genetic Identification and Implications of Another Invasive Species of Dreissenid Mussel in the Great Lakes

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In this paper we report the discovery and implications of a second nonindigenous species of dreissenid mussel in the Great Lakes. This species was detected in a routine screening of zebra mussels (*Dreissena polymorpha*) for allozyme variability. The two species differ at allozyme loci (Nei's $I = 0.30$ using 12 loci) and in their shell morphology (the second species lacks the acute angle, or carina, between the ventral and dorsal surfaces of the shell of the zebra mussel). As a working name, at least until its species identity is discovered, we have called the new species the "quagga mussel." Currently, this mussel occurs in Lake Ontario in equal frequencies with *D. polymorpha*. Its low frequency of occurrence in neighboring waters (e.g. the Erie canal, Niagara River, and outlet to Onondaga Lake) and lack of occurrence in any of the other Great Lakes suggest that (1) its point of introduction to North America was in Lake Ontario and (2) its range may expand.

Les auteurs signalent la découverte d'une seconde espèce exotique de moule de la famille des Dreissenidés dans les Grands Lacs et examinent les répercussions de cette découverte. L'espèce a été identifiée lors d'essais courants sur la variabilité des allozymes de la moule zébrée (*Dreissena polymorpha*). Les deux espèces se distinguent par les différents loci des allozymes (Nei's $I = 0,30$ à 12 loci) et morphologie de la coquille (la nouvelle espèce ne montrant pas l'angle aigu, ou carène, que montre la coquille de la moule zébrée entre la face ventrale et la face dorsale). Jusqu'à ce que cette nouvelle espèce soit identifiée, les auteurs lui donnent le nom vernaculaire anglais «quagga mussel». À l'heure actuelle, elle est retrouvée dans le lac Ontario à une fréquence semblable à *D. polymorpha*. Sa faible fréquence dans les eaux voisines (par ex., le canal Érié, la rivière Niagara et l'émissaire du lac Onondaga) et son absence dans les autres Grands Lacs portent à croire que le lac Ontario est le point d'introduction de l'espèce en Amérique du Nord et que son aire de répartition peut s'agrandir.

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In contrast with terrestrial systems, relatively few of the exotic species introduced to North American freshwater systems have achieved serious pest status. This situation is rapidly changing as the advent of cleaner harbors, cleaner ballast water, and faster transoceanic shipping facilitates the transport of species between continents (Mills et al. 1991). In the Great Lakes alone, five species have been introduced in the past 6 yr, of which four have been predicted to have detrimental effects on the ecosystem (ruffe (*Gymnocephalus cernuus*), round goby (*Neogobius melanostomus*), spiny water flea (*Bythotrephes cederstroemi*), and zebra mussel (*D. polymorpha*)). The zebra mussel, which arrived in Lake St. Clair in 1986 (Hebert et al. 1989), has already cost many thousands of dollars in damage due to clogged water pipes and industrial machinery. Phytoplankton populations in Lake Erie appear to have severely declined, presumably as a consequence of grazing pressure by these filter-feeding mussels. The rapid spread of the zebra mussel throughout the Great Lakes and inland waterways has dramatically increased awareness of the vulnerability of freshwater ecosystems to introduced pest species. Research on the basic biology of these nuisance species is an essential prelude to the development of effective control methods and for predicting the ecological impacts of their invasions.

The first and most important response to a newly introduced pest is to determine the species identity of the invader and its geographic origin. Once this information is known, data about the ecological requirements and natural biological controls of the pest species can be sought from its country of origin. North American researchers and utilities were able to rapidly forecast the scope of the zebra mussel problem, and take steps to minimize damage, because they had access to information about the mussels from European literature. Hence, one of the first documents published on zebra mussels in North America was an extensive review of the European literature on zebra mussel life history, ecological requirements, and methods of control (Mackie et al. 1989).

The long history of failures and successes in terrestrial pest management has clearly indicated the dangers of making assumptions about uniformity among populations of a single species (e.g. Compere 1961; Kumar 1984). For example, narrow-spectrum controls such as taxon-specific pathogens and physiological agents may not work on more than one species or genetic clone (Horber 1966; Metcalf and Luckmann 1975). The high genetic variability of zebra mussels (Hebert et al. 1989) suggests that genetically differentiated populations of mussels could exist which might vary in their ecological tolerances and response to control methods. During a study to

determine whether such differentiated populations exist within North America, we discovered the presence of a second dreissenid species in the Great Lakes which resembles *D. polymorpha*. This species has not been noted previously in the Great Lakes. Awareness of the presence of this second species is important for researchers working on zebra mussels, as the two species may not have similar ecological requirements and may not respond similarly to control methods. The purpose of this paper is to describe the genetic and morphological differences between these two species and to discuss the implications of this finding.

Methods

As part of an ongoing study to examine genetic differences among zebra mussel populations in North America, we examined mussels from Lake Erie, Lake Ontario, Lake Huron, Lake Michigan, Lake St. Clair, the Hudson River, and the Erie Canal using horizontal starch-gel electrophoresis. Mussels were frozen on dry ice or in liquid nitrogen within a few hours after collection in the field. All specimens were shipped to the Cornell Laboratory for Ecological and Evolutionary Genetics and stored at -70°C until processed. Extracts of whole mussels and one valve from each specimen were prepared. Half shells from each mussel were saved for later morphological analysis. Electrophoretic procedures, staining recipes, and nomenclature followed May (1992). An initial screen of 55 enzyme systems revealed 21 polymorphic loci with resolvable bands which could be reliably interpreted in zebra mussels. Twelve of these loci were used in the present study: diaphorase 1.6.2.2 (*Dia*), esterase 3.1.1.1 (*Est-1*), formaldehyde dehydrogenase (glutathione) 1.2.1.1 (*Fdh-1*), glyceraldehyde-3-phosphate dehydrogenase 1.2.1.12 (*Gapdh*), glucose-6-phosphate isomerase 5.3.1.9 (*Gpi*), isocitrate dehydrogenase 1.1.1.42 (*Idh*), malate dehydrogenase 1.1.1.37 (*Mdh-1,2*), phosphogluconate dehydrogenase 1.1.1.44 (*Gpd*), phosphoglucomutase 5.4.2.2 (*Pgm-1*), inorganic pyrophosphatase 3.6.1.1 (*Pp*), and triosephosphate isomerase 5.3.1.1 (*Tpi*). Forty to 80 individuals from each population were examined at these loci. Data were analyzed using "Genes in Populations," a software package designed by B. May and C. Krueger and written in C by W. Eng. Genetic distances were measured using Nei's genetic index (Nei 1972), and a dendrogram was generated using the UPGMA method of cluster analysis.

Results

In August 1991, a single mussel was found in a sample from the Erie Canal near Palmyra, New York, which did not have genotypes corresponding to those identified in zebra mussels. This individual also possessed a shell which was different from the common zebra mussel morphotypes we had observed. The shell lacked the carina, or acute angle between the ventral and dorsal surfaces (Fig. 1). In November, we obtained a sample of 99 mussels collected from Lake Ontario near Rochester, New York, which contained 47 mussels that were readily separable from the zebra mussels on the basis of their shell shape. All 47 of these mussels had consistent non-zebra mussel genotypes for *Pp*. Because the common name "zebra mussel" does not distinguish among members of the genus *Dreissena*, we used the name "quagga mussel" to differentiate the second morphotype (the "quagga" is an extinct relative of the zebra with striping on the head and shoulders). We used the 12 loci identified above to quantify the differences between the two mussel types; at

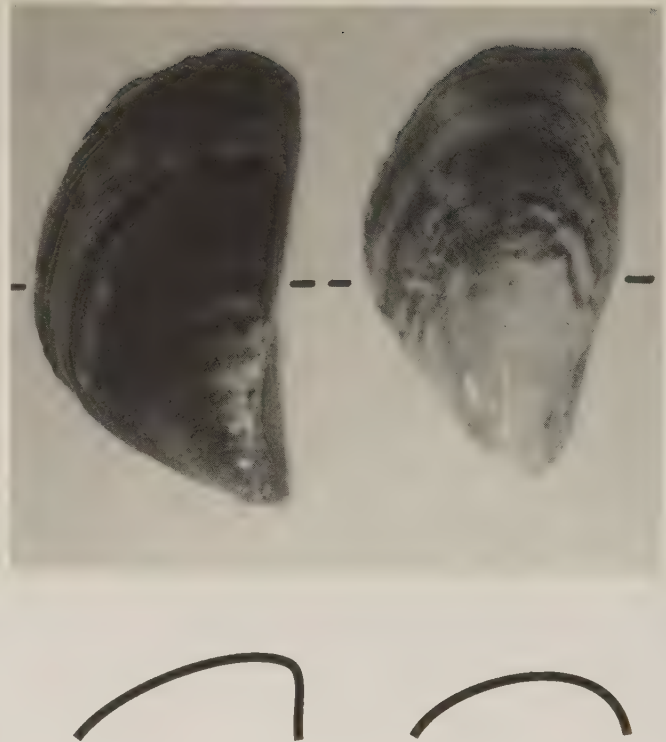


FIG. 1. Comparison of the shell morphology of zebra mussel (left) and quagga mussel (right). The broken line indicates the axes used for the cross-sectional profiles illustrated below.

other loci, the high amount of variability among both mussel types on the same gel made consistent scoring of bands difficult. Twenty-one quagga mussels were examined for these 12 loci to ensure a sufficient number of samples to determine the degree of relatedness between the two types of mussels. Fixed allelic differences between the zebra and quagga mussels existed at *Pp* and *Est*; unique alleles in the zebra mussels were present at all loci except *Fdh* and *Idh* (Table 1). The genetic distance between quagga and zebra mussels was 1.215 (Fig. 2). All six zebra mussel populations had heterozygosities above 0.3 at the 12 loci we examined, while the quagga mussel sample had less than one third that level of variability ($H_0 < 0.1$; Table 1).

Subsequently, quagga mussels were found in collections of mussels from Cape Vincent and Stony Island in Lake Ontario, the outlet from Onondaga Lake, and the Niagara River (Table 2). Quagga mussels have also been reported from the upper St. Lawrence River (D. B. Conn, St. Lawrence University, Canton, NY 13617, pers. comm.). All quagga mussels which we examined were collected between August and December 1991. Within each population, quagga and zebra mussels overlapped in size, with the largest quagga mussels being more than 3 cm long (Fig. 3). No mussels were found with allozyme patterns intermediate (heterozygotes) between those of the quagga and zebra mussels, indicating that hybrids are not readily formed between the two mussels.

Discussion

Determination of systematic relationships in taxa with a high degree of morphological variation can be problematic. Use of genetic data for elucidating systematic relationships has gained widespread acceptance and has been used to differentiate spe-

TABLE 1. Allelic frequencies at 12 allozyme loci in six zebra mussel populations and one quagga mussel population.

		Population						
Locus	Allele	Lake St. Clair	Lake Erie	Lake Michigan	Erie Canal	Lake Huron	Lake Ontario	
							Zebra	Quagga
<i>N</i>		45	43	34	40	41	19	21
<i>Dia</i>	1	0.628	0.500	0.559	0.713	0.700	0.688	0.000
	2	0.116	0.179	0.147	0.063	0.075	0.125	1.000
	3	0.209	0.226	0.191	0.175	0.175	0.188	0.000
	4	0.035	0.048	0.059	0.025	0.013	0.000	0.000
	5	0.012	0.048	0.029	0.025	0.013	0.000	0.000
	6	0.000	0.000	0.015	0.000	0.025	0.000	0.000
<i>Est-1</i>	1	0.659	0.631	0.762	0.625	0.683	0.750	0.000
	2	0.341	0.369	0.238	0.375	0.317	0.250	0.000
	3	0.000	0.000	0.000	0.000	0.000	0.000	1.000
<i>Fdh-1</i>	1	0.841	0.887	0.879	0.850	0.915	0.933	0.025
	2	0.159	0.113	0.121	0.150	0.085	0.067	0.975
<i>Gapdh</i>	1	0.556	0.738	0.589	0.638	0.720	0.632	1.000
	2	0.411	0.250	0.393	0.363	0.280	0.342	0.000
	3	0.033	0.012	0.018	0.000	0.000	0.026	0.000
<i>Gpi</i>	1	0.389	0.274	0.353	0.300	0.341	0.250	0.000
	2	0.478	0.500	0.515	0.475	0.451	0.500	0.000
	3	0.122	0.202	0.103	0.175	0.159	0.222	0.357
	4	0.011	0.000	0.000	0.000	0.000	0.000	0.000
	5	0.000	0.024	0.015	0.038	0.037	0.028	0.024
	6	0.000	0.000	0.015	0.013	0.000	0.000	0.000
	7	0.000	0.000	0.000	0.000	0.012	0.000	0.000
	8	0.000	0.000	0.000	0.000	0.000	0.000	0.619
<i>Idh</i>	1	0.727	0.655	0.609	0.763	0.683	0.708	0.900
	2	0.273	0.345	0.391	0.238	0.317	0.292	0.100
<i>Mdh-1</i>	1	0.500	0.524	0.591	0.538	0.610	0.605	0.000
	2	0.500	0.476	0.409	0.463	0.390	0.368	1.000
	3	0.000	0.000	0.000	0.000	0.000	0.026	0.000
<i>Mdh-2</i>	1	0.867	0.798	0.868	0.888	0.866	0.842	0.000
	2	0.133	0.202	0.132	0.113	0.134	0.158	1.000
<i>Pgm-1</i>	1	0.875	0.866	0.880	0.936	0.902	1.000	0.000
	2	0.125	0.122	0.120	0.064	0.098	0.000	0.000
	3	0.000	0.012	0.000	0.000	0.000	0.000	1.000
<i>Pgd</i>	1	0.944	0.917	0.941	0.987	0.951	0.923	0.000
	2	0.056	0.083	0.000	0.000	0.049	0.077	0.967
	3	0.000	0.000	0.059	0.000	0.000	0.000	0.033
	4	0.000	0.000	0.000	0.013	0.000	0.000	0.000
<i>Pp</i>	1	1.000	1.000	1.000	1.000	1.000	1.000	0.000
	2	0.000	0.000	0.000	0.000	0.000	0.000	1.000
<i>Tpi</i>	1	0.589	0.702	0.641	0.700	0.683	0.583	0.765
	2	0.356	0.238	0.297	0.275	0.220	0.389	0.000
	3	0.044	0.036	0.016	0.025	0.049	0.000	0.176
	4	0.011	0.024	0.047	0.000	0.049	0.000	0.000
	5	0.000	0.000	0.000	0.000	0.000	0.028	0.059
Avg. H_s		0.364	0.372	0.359	0.328	0.334	0.327	0.097
Avg. H_0		0.369	0.402	0.342	0.311	0.347	0.312	0.097

cies in a variety of taxa (e.g. Smith and Robertson 1981; Bullini 1983; Davis 1983; Thorpe 1983). In particular, allozyme data have added a powerful tool in addition to conchology and comparative morphology for assessing relationships among molluscan fauna (Davis 1983). Conspecific populations tend to show genetic similarities (Nei's I) above 0.9 ($D < 0.1$), and congeneric species have I values between 0.25 and 0.85

($0.16 < D < 1.39$) (Avisé and Smith 1977; Davis 1983; Thorpe 1983). By these criteria, the zebra and quagga mussels, with a genetic similarity of $I = 0.30$ ($D = 1.215$), are unquestionably distinct, highly differentiated species.

The two species can be differentiated by examining the shell. The zebra mussel has a pronounced angle, or carina, between the ventral and dorsal surfaces whereas the quagga mussel has

Quagga Mussel

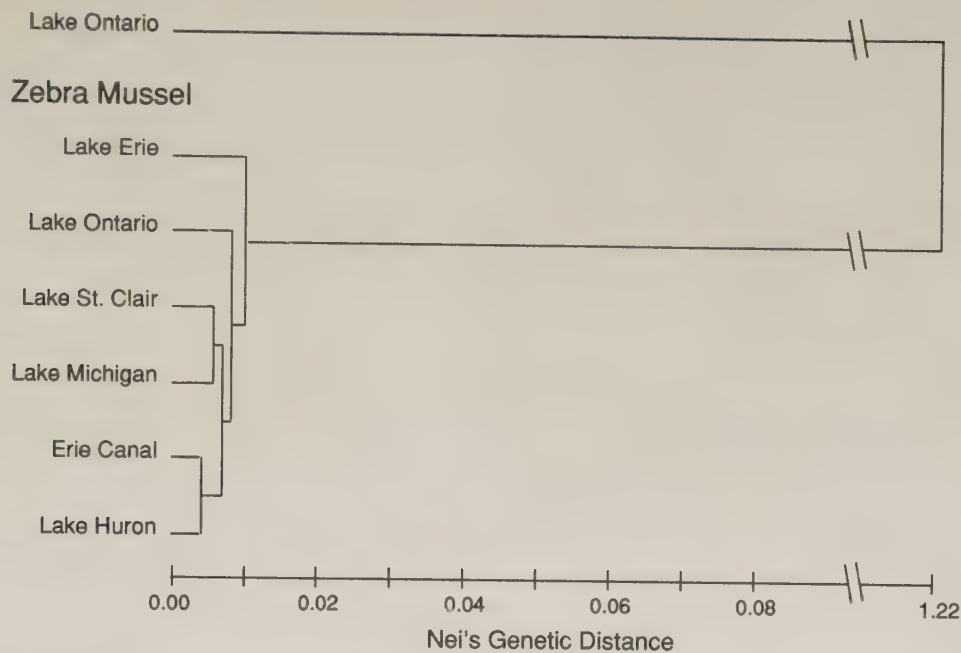


FIG. 2. Relative genetic distance dendrogram generated by UPGMA cluster analysis of Nei's (1972) genetic distance coefficients calculated between six zebra mussel samples and one quagga mussel sample using 12 polymorphic allozyme loci.

TABLE 2. Distribution of quagga mussels in the Great Lakes, with numbers of quagga and zebra mussels found in each collection.

Location	Body of water	Quagga mussels	Zebra mussels	Proportion of quaggas
Palmyra, NY	Erie Canal	2	>1000	<0.01
Brockport, NY	Erie Canal	2	100	0.02
Syracuse, NY	Onondaga outlet	4	500	<0.01
Niagara, Ont.	Niagara River	1	100	0.01
Stony Island, NY	Lake Ontario	12	11	0.52
Rochester, NY	Lake Ontario	47	52	0.47
Cape Vincent, NY	Lake Ontario	150	260	0.37

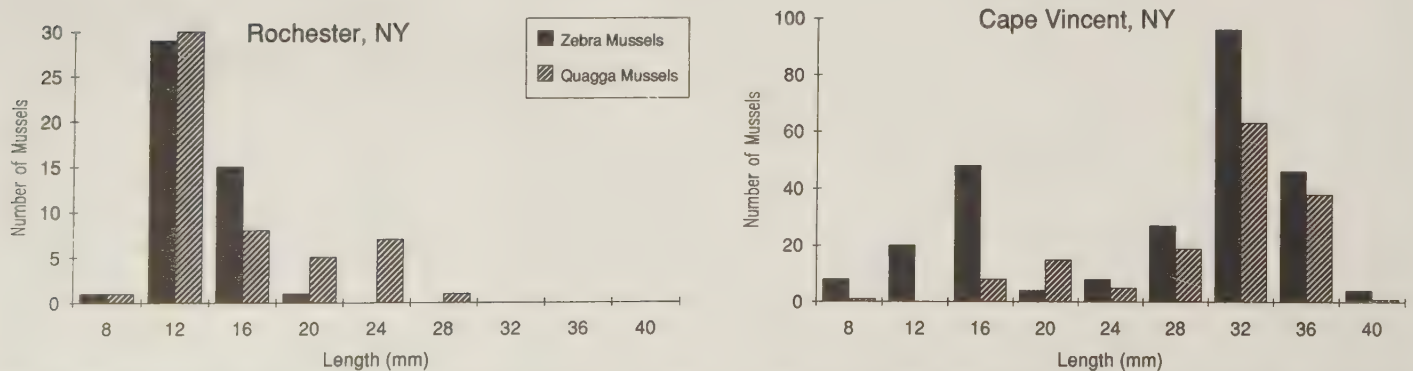


FIG. 3. Size range of quagga and zebra mussels collected from the central southern shore (Rochester) and the northeastern end (Cape Vincent) of Lake Ontario. The longest axis of each mussel was measured to the nearest millimetre.

a rounded carina and a bulging ventral surface (Fig. 1). Overall, quagga mussels appear to be laterally flattened when compared with zebra mussels. Both mussels have black and cream or white bands, although there is a wide variability in color pattern. Zebra mussels have shell patterns ranging from all cream to all black, including smooth stripes, jagged stripes, and individuals with a single, broad, longitudinal stripe. Not all of these pat-

terns have so far been seen in the quagga mussel; generally, the quagga banding patterns tend to consist of narrower and more numerous black lines than are seen on the zebra mussel. The quagga mussel does have one pattern which we have not yet noted in the zebra mussel during an extensive morphological study. This unique pattern consists of lateral black and white stripes, interrupted by a longitudinal white line. Until one is

familiar with both species, however, the normally wide intra-specific variability in shell shape and coloration can lead to uncertain identification. The most reliable character to separate the two species is the allozyme pattern of *Pp*. The two species are fixed for alternate alleles at this locus, and the bands are very distinct with different mobilities. The band for the quagga mussel has a faster rate of movement toward the anode than the band observed for the zebra mussel.

The obvious next task is to determine the species identity of the quagga mussel. Unfortunately, the taxonomy of the Dreissenidae is not well agreed upon. The classification of the family Dreissenidae began with the work of Andrussov (1897), who listed several species within the genus *Dreissena* and several varieties under *D. polymorpha*. In 1952, Zhadin reevaluated the family and listed seven species within *Dreissena*. In 1983, a Russian author listed three species in this genus (M. Ludyanskiy, Marine Biocontrol Corp., Sandwich, MA, pers. comm.), while a more recent review of the family named only two extant species: *D. (Dreissena) polymorpha*, currently established throughout western Europe, and *D. (Pontodreissena) rostriformis* from the Caspian Sea (Nuttall 1990). Nevertheless, *D. bugensis* is a commonly recognized species in the literature (e.g. Zolotareva et al. 1978). There does appear to be general agreement that, of the three extant genera within the family, both *Mytilopsis* and *Congeria* possess an apophysis or projection above the septum which members of the genus *Dreissena* lack (Nuttall 1990). The absence of an apophysis in all specimens of the quagga mussel we examined suggests that the quagga mussel is a member of the genus *Dreissena*. Illustrations in Zhadin (1952) and Nuttall (1990) suggest that several nominal species including *D. distincta* and *D. rostriformis* may be related to or synonymous with the quagga mussel. Clearly, unequivocal identification of the quagga mussel will require comparison of quagga genotypes, and possibly DNA sequence data, with data from putative species from Europe. In the process of this identification, the taxonomy of Dreissenidae may need to be reevaluated using both morphological and genetic characters.

The discovery of a second dreissenid species in the Great Lakes has an interesting parallel in the history of the invasion of another major freshwater pest species of mollusc, the Asian clam *Corbicula*. The Asian clam was accidentally introduced to the northwest coast of North America in 1924 and spread rapidly throughout the United States (McMahon 1983). Although the taxonomy of this group was, like *Dreissena*, "in a state of flux" (Hillis and Patton 1982), the invasive species was identified as *C. fluminea* on the basis of several morphological and ecological characters in combination with electrophoretic data (Britton and Morton 1979; Smith et al. 1979). Subsequently, however, a second morphotype was discovered in Texas, and electrophoretic studies showed that it was indeed a second species of *Corbicula* (Hillis and Patton 1982).

The date of arrival of the quagga mussel into the Great Lakes is difficult to determine. We suspect that, due to its limited distribution compared with that of the zebra mussel, the quagga mussel must have arrived more recently than the zebra mussel. The apparent absence of the quagga mussel from many sites we have sampled around the Great Lakes, in particular Lake St. Clair where the zebra mussel was first found, also suggest that the two species were introduced at different locations. Zebra mussels now comprise several size classes in Lakes Erie and St. Clair; these size classes can be broadly classified into year classes (Hebert et al. 1989, 1991). The bimodal size distribution of the zebra mussels at Cape Vincent suggests that two year

classes are present (Fig. 3). If the growth rates of two species are similar, the quagga mussels at this site are at least 2 yr old (i.e. they were spawned in 1989). This conclusion, and the broad distribution of the mussel throughout Lake Ontario, suggests that the quagga mussels have been present in North America since at least 1989.

Of interest is the significantly lower level of heterozygosity observed in the quagga mussels relative to zebra mussels (<0.1 versus >0.3 , respectively). While we report on only a single population of quagga mussels, the consistent level of heterozygosity observed among zebra mussel populations suggests that the level of heterozygosity observed in the quagga mussels is probably reasonably accurate. This lower level of heterozygosity implies either that (1) the progenitor (source) quagga population had a low level of heterozygosity or (2) there was a much smaller founding population for the quagga mussel than for the zebra mussel. In either case, although the quagga mussels may have different environmental tolerances than the zebra mussels, they have a much narrower genetic base for differential response to the environment.

The discovery of a second species of dreissenid mussel in the Great Lakes has several major ramifications. First and foremost, the finding of the quagga mussel underlines the importance of examining the basic biology of newly invasive pest species. The presence of the quagga mussel casts doubts on the validity of recent ecological studies, at least in Lake Ontario, that were based on the assumption that only the zebra mussel was present. Second, because two species rarely, if ever, overlap completely in their ecological requirements, the quagga mussel undoubtedly differs from *D. polymorpha* in some of its life history parameters. These differences may result ultimately in the two species having different ranges. Third, control measures against multispecies populations may be more complex than for single species. A more thorough understanding of the taxonomy and geographic origin of these two dreissenid species is needed to establish the features of their basic biology and ecological requirements. Only once these features have been established can the development of effective control strategies be undertaken. Fourth, this discovery begs the question as to whether or not even more species have been recently introduced. The 3-yr time lag before discovery of the quagga mussel suggests that the high morphological variability of this genus may deceive investigators into lumping all unusual types into the same species. The discovery of one additional species should serve to keep us alert to the possibility that other species may have already been introduced or could be introduced in the future.

Acknowledgments

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Tests of Genetic Stock Identification Using Coded Wire Tagged Fish

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Genetic Stock Identification (GSI) uses allozyme variation to determine the composition of mixed-stock fisheries. The GSI method was tested using real fishery data. We report, for the first time in the primary literature, results of tests of GSI in which source stock and ocean-caught mixture samples were separately obtained and the mixture composition was known exactly because the fish used were marked by Coded Wire Tags (CWTs). The accuracy of GSI and its dependence on the quality of genetic data were studied by computer experiments. Rare alleles, which could result from poor sampling procedures, can lead to significant estimation errors. Estimation accuracy depended on the concordance between stocks present in the baseline data and the mixture sample and on the number of loci used in the analysis. Two methods for computing the contributions of groups of source stocks were found to be comparable under most, but not all, conditions. In a blind test of GSI, stock group composition estimates had absolute errors of less than 3%. This suggests that the GSI method can produce accurate stock contribution estimates using real fishery data.

La méthode d'identification génétique des stocks se sert de la variation des allozymes pour établir la composition de pêcheries pluristocks. Les auteurs l'ont appliquée à des données actuelles sur la pêche et présentent les résultats obtenus pour la première fois dans une publication primaire. Ils ont pu identifier les échantillons tirés d'un stock source et les échantillons mélangés capturés en mer, et ont déterminé exactement la composition de ceux-ci car les poissons portaient des étiquettes métalliques codées. Les auteurs ont aussi étudié la précision de cette méthode d'identification et sa dépendance sur la qualité des données génétiques par l'entremise d'expériences informatiques. Les allèles rares, qui sont peut-être le résultat de méthodes d'échantillonnage inadéquates, peuvent être à la source d'importantes erreurs d'estimation. La précision de l'estimation dépendait de l'accord entre, d'une part, les stocks représentés dans les données de base et les échantillons mélangés et, d'autre part, le nombre de loci utilisés lors de l'analyse. Deux méthodes de calcul de la contribution de groupes de stocks sources ont été identifiées comme équivalentes dans presque toutes les conditions. Lors d'une épreuve à l'insu de la méthode d'identification génétique, l'erreur absolue des estimations de la composition du groupe de stock était inférieure à 3 %. Ceci porte à croire que cette méthode peut donner des estimations précises de la contribution d'un stock à partir de données actuelles sur la pêche.

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In recent years, some chinook salmon (*Oncorhynchus tshawytscha*) stocks have been depleted to the point that season closures have been imposed on commercial troll fisheries that exploit a mixture of hatchery and wild stocks (Fraidenberg and Lincoln 1985; Pacific Fishery Management Council (PFMC) 1986). Mark-recapture techniques can provide estimates of the contributions of hatchery stocks to the fishery har-

vest, but unless expensive and extensive marking programs are undertaken, the relative contributions of wild stocks to the harvest remain unknown. Without this information, it is difficult to assess the effectiveness of management actions designed to protect depleted wild stocks or to prevent overescapement of abundant wild stocks. Thus, developing the capacity to directly estimate the contributions of wild stocks in mixed-stock fisheries has enormous potential application.

Genetic Stock Identification (GSI) (Grant et al. 1980; Milner et al. 1981; Miller et al. 1983; Milner et al. 1983; Beacham et al. 1985; Milner et al. 1985; Beacham et al. 1987; Pella and Milner 1987; Utter et al. 1987, 1989; Shaklee et al. 1990b) has emerged as one means to distinguish stocks of salmon and directly estimate the composition of mixed-stock fisheries. In

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TABLE 1. Sets of loci used to analyze the stock composition of mixture samples (locus nomenclature follows Shaklee et al. (1990a); an asterisk denotes that a locus is present in the set).

Locus	Locus sets		
	11-locus	15-locus	35-locus
sAAT-1,2			*
AAT-3			*
mAAT-1			*
mAAT-2			*
ADA-1			*
AH-1			*
mAH-3			*
mAH-4			*
DPEP-1	*	*	*
EST-3	*		
GPI-1	*	*	
GPI-2	*	*	*
GPI-3	*	*	
GPIH			*
HAGH			*
IDH-2			*
IDH-3			*
IDH-4	*	*	*
LDH-4	*	*	*
LDH-5			*
MDH-1,2	*	*	*
MDH-3,4	*	*	*
mMDH-1			*
MDHp-1			*
MDHp-2			*
MPI	*	*	*
PDPEP-2			*
PEPLT			*
PGDH	*		*
PGK-2			*
PGM-1	*		*
PGM-2	*		*
SOD-1	*	*	*
TAPEP-1	*	*	*
TPI-3			*
TPI-4			*
PGM-3			*
PGM-4			*

contrast with expensive mark-recapture techniques, GSI exploits inherent genetic differences among fish stocks to estimate the relative proportion of each in a representative sample from the mixed-stock fishery (mixture sample). In order to use GSI to assess mixed-stock fishery composition, genotypic or allelic frequency data from all stocks that are believed or known to contribute to the mixture are required. The set of genetic data for all potentially contributing stocks constitutes the "baseline data" (Milner et al. 1985). Given the baseline data and corresponding genetic data for the mixture sample, a computer-based estimation procedure is applied to calculate the most likely stock composition of the mixture.

In this paper, we test the ability of GSI to determine the stock composition of mixtures of chinook salmon that were captured in the ocean troll fishery off the coasts of California and southern Oregon. In this case, the fish in the mixture were collected independently of the baseline data. Chinook salmon used in this study had been marked with Coded Wire Tags (CWTs); therefore, their stock of origin was known. Given this information, we could perform mixture analyses on mixture samples of known stock composition to explore how different uses of the

genetic data affected the accuracy of stock composition estimates.

In addition, we provide results concerning a "blind test" of GSI in which the mixture analysis was performed without prior knowledge of the composition of the sample. Such a blind test insured integrity of the analysis. This represents the first such test to be reported in the primary literature, although similar tests appear elsewhere (Milner et al. 1981).

Methods

In general, the application of GSI to determine the stock composition of a mixed-stock fishery involves three phases: (1) the collection and genetic description of baseline data from stocks that could be present in a mixed-stock fishery (baseline samples), (2) the genetic description of a representative sample collected from the mixed-stock fishery (mixture sample), and (3) the estimation of the most probable stock composition of the sample from the mixed-stock fishery using the method of maximum likelihood (mixture analysis). A detailed description of each phase as implemented in this paper follows.

Genetic Description

Allozyme analysis provided genetic descriptions of baseline and mixture samples. Samples of eye, heart, liver, and muscle tissue were collected from fall-run juvenile chinook salmon for all of the baseline samples except the Upper Sacramento River sample, which consisted of winter-run juveniles. Samples of eye and muscle tissue were collected from legal-sized adult chinook salmon for the mixture samples. The tissue samples for the baseline data were assayed at up to 124 isozyme loci using allozyme electrophoresis (Aebersold et al. 1987). We required that information on loci be present in all baseline samples and in at least some fish in the mixture sample for all loci used in stock composition analyses. Thus, due to the tissue-dependent expression of loci, only the subset of loci for which allelic variation could be detected from either muscle or eye tissue was used for GSI. Prior to 1987, this requirement limited the number of available loci to 15 loci (Table 1), but by 1987, 35 loci met this criterion (Table 1).

Baseline Samples

In the absence of prior information about which stocks in the set of baseline data are contributors, it is prudent to consider every stock to be a potential contributor. For the application of GSI to Pacific salmon (*Oncorhynchus* spp.), each "stock" should ideally represent a more or less discrete, self-sustaining breeding unit spawning at a given time and place within a lake or stream (Ricker 1972). Since we lacked conclusive evidence about whether or not each baseline sample constituted a stock under this definition, we considered samples from different collection sites to constitute samples from individual source populations (source stocks). Our use of the term "stock" also contrasts with another definition as a fish population in Hardy-Weinberg equilibrium (Booke 1981) that facilitates the computation of genotype probabilities required for stock composition analyses (cf. Fournier et al. 1984). Nonetheless, our usage is consistent with the purpose of testing whether the GSI method can accurately determine the contributions of groups of source stocks from various rivers to mixtures composed of ocean-caught fish with known stocks of origin.

The baseline data used in this paper consist of source stock samples collected from streams ranging from California to

TABLE 2. Baseline data used to analyze stock composition in tests using the 1986 CWT sample (26-stock baseline) and in the blind test using the 1988 CWT sample (37-stock baseline).

River system	Source stocks	Sample size in baseline data set	
		26-stock	37-stock
Eel River	Hollow Tree Creek	—	100
	Middle Fork Eel River	105	95
	Outlet Creek	51	—
	Redwood Creek (on Eel River)	—	93
	Salmon Creek	—	96
	South Fork Eel River	140	99
	Tomki Creek	50	—
	Van Duzen River	—	100
Klamath River	Blue Creek	—	100
	Bogus Creek	40	128
	Camp Creek	—	106
	Horse Linto Creek	—	100
	Irongate Hatchery	102	99
	Omagar Creek	—	100
	Salmon River	—	99
	Scott River	50	—
	Shasta River	120	100
	South Fork Trinity River	93	100
	Trinity River Hatchery	170	120
Mad River	Mad River Hatchery	96	99
	North Fork Mad River	—	61
Mattole River	Mattole River	72	100
Redwood Creek	Prairie Creek Hatchery	99	—
	Redwood Creek	96	95
	Redwood Creek Lagoon	—	100
Sacramento River	Bear River	73	—
	Coleman Hatchery	303	100
	Feather River Hatchery	107	100
	Merced River Hatchery	114	100
	Murphy Creek	54	—
	Nimbus Hatchery	—	100
	Sacramento River	105	—
	Secret Ravine	29	—
	Stanislaus River	32	—
	Tuolumne River	96	—
	Upper Sacramento River	—	94
	Yuba River	190	—
Smith River	Rowdy Creek Hatchery	105	62
	Smith River	58	—
	Middle Fork Smith River	—	99
Alsea River	Fall Creek Hatchery	—	100
Chetco River	Chetco River Hatchery	—	100
Coos River	Millacoma River	—	100
	Morgan Creek Hatchery	—	100
Coquille River	South Fork Coquille River	—	100
Elk River	Elk River Hatchery	—	100
Rogue River	Rogue River	—	100
	Applegate River	—	100
Umpqua River	Rock Creek Hatchery	—	100

British Columbia. The data were grouped according to sample collection date. Samples collected prior to 1987 and reported by Bartley and Gall (1990) and Gall et al. (1989) are the "26-stock" baseline data (Table 2) whereas samples collected during 1987 or 1988 are the "37-stock" baseline data (Table 2; see Gall et al. 1989, 1992 for details).

In 1986, we acquired data for 85 source stocks in Oregon, Washington, and British Columbia from the U.S. National Marine Fisheries Service (NMFS). These samples will be called the "coast-wide" baseline data (see Gall et al. 1989 for details); the NMFS acts as a repository for the data. The combined data from the 26-stock and the coast-wide baseline are the "111-

stock" baseline data, while the "48-stock" baseline consists of all California and coastal Oregon stocks within the 111-stock baseline. Four variable loci in the 26-stock baseline were not measured in all samples in the coast-wide baseline, and consequently there were 11 loci available for mixture analysis with the 111-stock baseline (Table 1).

Mixture Samples

Mixture samples consisted of adult chinook salmon marked with CWTs (Jefferts et al. 1963) captured during the ocean troll fisheries off the coasts of California and Oregon in 1986 and 1988 (the 1986 CWT sample and the 1988 CWT sample, respectively). The 1986 CWT sample consisted of 1628 fish; 1163 fish collected by the Oregon Department of Fish and Wildlife (ODFW) and 465 fish collected by the California Department of Fish and Game (CDFG). The stock of origin for each sample was assigned using the PFMC publication "Pacific Salmonid Coded Wire Tag Releases Through 1986" to interpret tag codes. A summary of the geographic origins of fish in the 1986 CWT sample is provided in the Appendix. The 1988 CWT sample contained 220 fish collected by CDFG.

Mixture Analysis

The stock composition of a given mixture sample was estimated using the method of maximum likelihood conditioned on the baseline data being known exactly (Fournier et al. 1984). The EM algorithm (Dempster et al. 1977; Milner et al. 1981) was used to compute stock composition estimates with a cutoff parameter of 10^{-5} (that is, iteration stopped when the absolute value of the maximum difference between elements of successive iterates differed by less than the cutoff parameter). Hardy-Weinberg equilibrium and independence of loci were also assumed (Bartley and Gall 1990; D. M. Bartley, unpubl. data). An individual CWT fish was excluded from the mixture analysis when the probability of observing its genotype was less than 10^{-7} for all baseline stocks (the value 10^{-7} was selected empirically to ensure that round-off error did not affect our computations). Such fish have "improbable genotypes" relative to the baseline data being used, and, although the likelihood that a given fish will have an improbable genotype increases as the number of loci used for analysis increases, these fish are outliers relative to the baseline data used for mixture analysis. Standard deviation estimates reported for the blind test were computed using the infinitesimal jackknife covariance estimator (Millar 1987).

When large numbers of source stocks are potential contributors to a mixed-stock fishery, it is often necessary to summarize their contribution estimates into a composite "stock group" estimate to be able to apply the results. In this case, the goal of mixture analysis is to estimate the stock group contribution accurately, and estimating the source stock contributions becomes an intermediary computation.

Two approaches to computing estimates for stock groups were examined: the "allocate and sum" and the "pool and allocate" procedures (Wood et al. 1987). In the allocate and sum procedure, estimates of the contribution of individual source stocks to the mixture are computed first. Individual contribution estimates are then summed to produce the estimate of each stock group's contribution. In the pool and allocate procedure, a composite stock is formed for each stock group by pooling allele frequencies of all stocks within the stock group. The stock group's contribution is then estimated using the composite stock. In this paper, allele frequencies for composite

stocks were computed as the unweighted average of the allele frequencies for the constituent stocks. We chose the unweighted average, which assumes that constituent stocks contribute equally to the group, because for many stocks, estimates of total population size, spawning escapement, or other indices of relative stock abundance were not available to suggest alternative weights.

Results

Preliminary Examination of the Method

Preliminary analyses were performed using the 1986 CWT sample with the 26-stock baseline data to examine the potential utility of the GSI method to assess the stock composition of chinook troll fisheries off the coasts of California and Oregon. To evaluate the results, each source stock in the baseline data and each fish in the 1986 CWT sample was assigned to a geographic group based on the location of its river of origin (Table 2; Appendix). The geographic groupings of stocks were the *Sacramento group*, consisting of stocks originating in the Sacramento River and San Joaquin River; the *Middle coast group*, consisting of stocks originating in the Eel, Mad, or Mattole River; the *North coast group*, consisting of stock from the Klamath or Smith River and Redwood Creek (on the California coast); the *Oregon group*, consisting of stocks originating in coastal Oregon rivers; the *Washington/Columbia group*, consisting of stocks originating in Puget Sound, Washington, coastal rivers, or the Columbia River; and the *Canadian group*, consisting of stocks originating in British Columbia rivers (Table 2). By assigning each source stock and fish to one geographic group, we could compare the accuracy of estimated and actual contributions of each geographic group to the mixture sample. In fact, some grouping by geographic proximity was essential to the interpretation of test results because several source stocks were not matched by fish in the 1986 CWT sample. Conversely, several fish in the 1986 CWT sample were not matched by source stocks in the baseline data.

Several mixture analyses were performed with the 26-stock baseline to see whether estimated stock group contributions were accurate. In one analysis, the contributions for a subsample consisting of data for 725 CWT fish all originating from California stocks were estimated using the 26-stock baseline (Table 2). This explored how the estimation procedure would perform in a best-case scenario where the mixture sample consisted of a subset of the stocks present in the baseline. Thirty loci were used (sAAT-1,2, sAAT-3, AH-1, AK-1, CK-1, CK-2, DPEP-1, EST-3, EST-4, EST-5, G3PDH-1, G3PDH-2, GPI-1, GPI-2, GPI-3, GPIH, IDH-3, IDH-4, LDH-4, LDH-C, MDH-1,2, MDH-3,4, MDHp-1, MPI, PGDH, PGK-2, PGM-1, PGM-2, SOD-1, and TAPEP-1) and the results suggested that the methodology would work well. Estimated contributions for the Sacramento, Middle Coast, and North Coast stock groups were 0.327, 0.098, and 0.575, respectively, while the actual contributions were 0.330, 0.077, and 0.593. Thus, the largest absolute error in any contribution estimate was about 2%.

Despite these promising results, the 26-stock baseline data set was limited because it contained no source stock samples collected outside California. Therefore, whenever non-California stocks were present in a mixture sample, the use of the 26-stock baseline would misallocate the contributions of non-California stocks to California stocks. To remove this limitation, we used the 111-stock baseline to perform further analyses using the 1986 CWT sample. However, some of these

TABLE 3. Summary of sets of loci, baseline data, and mixture sample data used in tests involving the 1986 CWT sample (an asterisk denotes that the set of data was used in a particular test).

Test	Locus set		Baseline data			Mixture sample	
	11-locus	15-locus	26-stock	48-stock	111-stock	All	California ^a
1	*		*	*	*	*	
2	*		*				*
3		*	*				*
4		*	*				*

^a The subsample of 926 CWT fish of California origin.

TABLE 4. Results of Test 1 examining the effect of applying different portions of the 111-stock baseline on estimation accuracy (NE denotes that no estimate of this stock group's contribution was made, since it was assumed that the group does not contribute to the mixture sample).

Stock group	Estimated contribution by baseline data set			
	Actual contribution	111-stock	48-stock	26-stock
Eel	0.051	0.045	0.044	0.041
Klamath	0.352	0.332	0.300	0.449
Mad	0.000	0.000	0.000	0.000
Mattole	0.000	0.000	0.000	0.000
Redwood	0.000	0.000	0.003	0.165
Sacramento	0.166	0.036	0.148	0.346
Smith	0.000	0.000	0.000	0.000
Oregon	0.400	0.371	0.505	NE
Columbia	0.030	0.091	NE	NE
Washington	0.001	0.000	NE	NE
BC	0.000	0.125	NE	NE
Puget Sound	0.000	0.000	NE	NE

analyses produced unexpectedly poor results. In particular, one analysis that applied the 111-stock baseline to the entire 1986 CWT sample produced very large estimation errors for the Washington/Columbia and Oregon stock groups. Most of the misallocation resulted from a gross overestimate (estimate 49%, actual <1%) of the contribution of one stock, the Priest Rapids – Hanford stock, which belonged to the Washington/Columbia stock group. The cause of this overestimate was traced to the rare LDH-C*70 allele at the LDH-C locus, which represented genetic variability now recognized to be an artifact of poor tissue quality. The LDH-C*70 allele had never been observed in baseline samples analyzed at the University of California, Davis (UCD) laboratory, although it was scored for some fish in the 1986 CWT sample and was present at low frequency in two Columbia River stocks (Priest Rapids – Hanford and Ice Harbor – Lyons Ferry). Further investigation showed that improper handling of some of the CWT fish had led to tissue degradation and misinterpretation of the common LDH-C*100 allele as the LDH-C*70 allele. Since the LDH-C*70 allele was only present in the Priest Rapids – Hanford and Ice Harbor – Lyons Ferry stocks, fish with this allele in the 1986 CWT sample could only be allocated to one of these two baseline stocks under the standard GSI model. This led to a large overestimate of the Priest Rapids – Hanford contribution in the mixture analysis. More importantly, this analysis demonstrated the necessity of consistent data interpretation and of proper handling of tissue samples for the successful application of the GSI method.

Computer Experiments Using the 1986 CWT Sample

Following a thorough reexamination of the 1986 CWT sample, a number of computer experiments (Table 3) were performed to examine how estimation accuracy depended on the selection and application of the available data. In each of our tests, stock contribution estimates were compared with actual sample composition, and the reported error was the difference between the estimated and actual stock group contribution.

The tests focussed on three targeted groups of stocks: those from the Eel, Smith, and Klamath rivers (Gall et al. 1989). Eel and Smith stocks were important because little information on ocean productivity and spawning escapement is available for these stocks (spawning stock surveys are available for only two minor tributaries of the Eel River; PFMC 1991). Klamath River stocks were important because the rebuilding, conservation, and harvest allocation among user groups of these stocks have been contentious and much debated in recent years (Fraidenberg and Lincoln 1985; McEvoy 1986). In fact, measures to reduce the ocean harvest of Klamath River stocks have included season closures as well as other restrictions on the commercial salmon troll fishery in the Klamath Management Zone (KMZ), an area of the Pacific Ocean extending from Point Delgada, California, to Cape Blanco, Oregon, where the commercial chinook harvest was well below historic levels throughout much of the 1980's (PFMC 1986; PFMC 1991, fig. II-4).

Effect of baseline stock choice (Test 1, Table 4)

The choice of stocks that are included in the baseline data is an a priori assumption that may affect estimation errors. This effect is most pronounced when the mixture sample contains stocks that are not present in the baseline data set. In Test 1, three mixture analyses applied successively smaller baseline data sets to the largest possible mixture sample. Each analysis used the entire 1986 CWT sample and the 11-locus set of loci. The Washington/Columbia stock group was subdivided into three geographic groups: Columbia, Washington Coast, and Puget Sound. Similarly, the North coast group was subdivided into the Klamath, Redwood Creek, and Smith geographic stock groups, and the Middle coast group was subdivided into the Eel, Mad, and Mattole geographic stock groups. All stock group contribution estimates were summarized using the allocate and sum procedure.

First, we used the 111-stock baseline data to analyze the composition of the entire 1986 CWT sample (thereby effectively assuming that any of the 111 stocks were potential contributors to the mixture). Second, we excluded the British Columbia (BC), Washington, and Columbia River baseline data and used the 48-stock baseline to analyze the entire 1986 CWT sample. This analysis simulated the assumption that only stocks originating from river systems south of the Columbia River were potential contributors to the mixture and led to the deliberate

TABLE 5. Results of Test 2 comparing the effect of using the 11-locus and the 15-locus sets of loci with the 26-stock baseline.

Stock group	Actual contribution	Set of loci used for mixture analysis			
		11-locus		15-locus	
		Estimate	Error	Estimate	Error
Eel	0.090	0.113	0.023	0.089	-0.001
Klamath	0.617	0.600	-0.017	0.606	-0.011
Mad	0.000	0.000	0.000	0.000	0.000
Mattole	0.000	0.000	0.000	0.000	0.000
Redwood	0.000	0.021	0.021	0.031	0.031
Sacramento	0.293	0.266	-0.027	0.273	-0.020
Smith	0.000	0.000	0.000	0.000	0.000

underestimation of the Columbia River and Washington Coast contributions. In reality, a few fish from these groups were included in the mixture sample. This analysis explored the trade-offs in estimation accuracy that resulted from the assumed absence of the more northerly stock groups. Third, we explored how the contribution of non-California stocks would be misallocated to California-origin stocks when only the 26-stock baseline was used to analyze the comparison of the entire 1986 CWT sample.

The results (Table 4) demonstrate the importance of trying to match the baseline data with the mixture sample. The total error (the sum of the absolute estimation errors for all stock groups) was smallest (0.22) when the 48-stock baseline was used. In contrast, the use of the 111-stock and 26-stock baseline data sets led to total errors of 0.37 and 0.88, respectively. While the GSI method will misallocate the contributions of stocks present in the mixture sample but not present in the baseline data, the exclusion of relatively minor contributors may improve the match between stocks present in the baseline data and the mixture sample and can, in some instances, actually improve estimation accuracy.

Comparing the 11-locus and 15-locus sets of loci (Test 2, Table 5)

In Test 2, we examined whether the exclusion of genetic data would affect the accuracy of stock composition estimates. For this, we used a mixture consisting of fish originating in California. As described above, when the coast-wide baseline data were added to our 26-stock baseline data, the number of loci available for analysis was reduced from 15 to 11. The four loci no longer available were EST-3, PGDH, PGM-1, and PGM-2 (Table 1). Of these four, only PGM-2 was both a highly variable and a easily resolvable locus. A priori, it was not clear whether estimation accuracy would be lost through the use of this 11-locus loci when only California-origin stocks were present in both the baseline and the mixture sample. Thus, we analyzed the mixture consisting of all 926 California-origin fish in the 1986 CWT sample using the 26-stock baseline and both sets of 15 or 11 loci.

The test results (Table 5) show that the total estimation error was only slightly larger (0.09 versus 0.06) when the 11-locus set of loci was used. Note, however, that the contribution of Redwood Creek was actually estimated less accurately when the larger set of loci was used. Thus, the inclusion of more loci need not uniformly reduce estimation accuracy.

Effect of stock grouping on the pool and allocate procedure (Test 3, Table 6)

In Test 3, we examined whether different stock groupings would affect estimation accuracy when the pool and allocate

TABLE 6. Results of Test 3 comparing the effect of using different stock groupings with the pool and allocate procedure.

Stock group	Actual contribution	Estimate	Error
<i>Using 3 stock groups</i>			
Coastal ₅	0.090	0.125	0.035
Klamath	0.617	0.602	-0.015
Sacramento	0.293	0.273	-0.020
<i>Using 5 stock groups</i>			
Coastal ₅	0.000	0.000	0.000
Eel	0.090	0.081	-0.009
Smith	0.000	0.080	0.080
Klamath	0.617	0.576	-0.041
Sacramento	0.293	0.262	-0.031
<i>Using 7 stock groups</i>			
Eel	0.090	0.027	-0.063
Mad	0.000	0.018	0.018
Mattole	0.000	0.000	0.000
Redwood Creek	0.000	0.026	0.026
Smith	0.000	0.090	0.090
Klamath	0.617	0.576	-0.041
Sacramento	0.293	0.264	-0.029

procedure was applied (Table 6). The stock groups were chosen to reflect the importance of the Eel, Klamath, and Smith stocks, as well as other stocks originating in California coastal rivers. In particular, the three analyses in this test focussed on stocks originating in northern California coastal streams which are important contributors to the KMZ (PFMC 1991) and for which an exploration of the effects of stock grouping was considered important. Each analysis used a subsample of the 1986 CWT sample consisting of California-origin fish so that the 15-locus loci set could be used. All stock groups were formed by pooling allele frequency data. (A corresponding analysis using the allocate and sum procedure was applied in Test 2 (Table 5).)

For the first analysis, the California-origin source stocks were grouped into three stock groups: Coastal₅, Klamath, and Sacramento. These three stock groups represented a coarse level of pooling for the 26-stock baseline and eliminated the possibility of estimating the Eel and Smith contributions separately. The Coastal₅ composite stock consisted of the pooled allelic data for the source stocks from the Eel, Mad, Mattole, and Smith rivers and Redwood Creek (Table 2). The Klamath com-

posite stock consisted of the pooled allelic data for the source stocks from the Klamath-Trinity drainage. The Sacramento composite stock consisted of the pooled allelic data for the source stocks from the Sacramento – San Joaquin drainage. We next grouped the California source stocks into five stock groups so that estimates of the Eel and Smith contributions could be made. Two additional stock groups were defined by dividing the Coastal₅ stock group into three smaller groups (Coastal₃, Eel, and Smith). The Eel and Smith stock groups consisted of source stocks from the Eel and Smith rivers, respectively, while the Coastal₃ group included source stocks from the Mad and Mattole rivers and Redwood Creek. Finally, we formed seven stock groups by splitting the Coastal₃ group into the Mad and Mattole River and Redwood Creek stock groups. This analysis with seven groups explored whether estimation accuracy would be increased by attempting to estimate the contributions of the remaining coastal rivers separately.

The smallest total error (0.07) was obtained when three stock groups were used (Table 7). Total error more than doubled to 0.16 and 0.27 when five and seven stock groups were used, respectively. To some extent, the increase in estimation error is due to the additional number of parameters that must be estimated when five or seven stock groups are used. The trade-off, however, was that no direct estimates of the relative contributions of source stocks originating in the Eel and Smith rivers could be made when only three stock groups were used.

Comparing the allocate and sum and pool and allocate procedures (Test 4, Table 8)

We performed three comparisons of the accuracy of the allocate and sum and the pool and allocate procedures (Table 8). Each comparison used the 15-locus set of loci. First, we compared the allocate and sum and pool and allocate procedures under the best circumstances, that is, when stocks present in the mixture sample matched the stocks present in the baseline.

This comparison used the subsample of the 1986 CWT sample consisting of California-origin fish and the 26-stock baseline. Second, we compared the two procedures when the Eel River stock group was absent from the mixture sample but was present in the baseline. In this case, we analyzed the subsample of the 1986 CWT sample consisting of California-origin fish with the samples originating in the Eel River drainage removed using the 26-stock baseline. Third, we compared the procedures when the Klamath River stock group was absent from the mixture sample but was present in the baseline. For this, we used the subsample of the 1986 CWT sample consisting of California-origin fish with the samples originating in the Klamath River drainage removed and the 26-stock baseline. The objectives of these two comparisons were to determine if the GSI method could detect the absence of Eel or Klamath River stocks and to compare relative performance of the allocate and sum and pool and allocate procedures under these circumstances. A corresponding comparison could not be made using data for the Smith River, since there were no CWT samples from this river.

We found that, under the best circumstances, the estimated stock group contributions were extremely accurate (total errors <0.04) and that either method of pooling data worked well. When the Eel River stocks were excluded from the mixture sample but included in the baseline data, the allocate and sum procedure (total error 0.09) was more accurate than the pool and allocate procedure (total error 0.22) but more severely overestimated the contribution of the Eel River stock group. Similarly, when the Klamath River stocks were excluded from the mixture sample but included in the baseline data, the allocate and sum procedure (total error 0.28) was more accurate than the pool and allocate procedure (total error 0.35), but only marginally so and once again more severely overestimated the Klamath stock group contribution. Obviously, a stock presumed to be in a mixture sample which is actually not present may be

TABLE 7. Results of Test 4 comparing the allocate and sum and the pool and allocate procedures for summarizing stock group contributions.

Stock group	Actual contribution	Pooling procedure			
		Allocate and sum		Pool and allocate	
		Estimate	Error	Estimate	Error
<i>Best circumstances: stocks in the baseline data and mixture sample match</i>					
Eel	0.090	0.106	0.016	0.109	0.019
Klamath	0.617	0.617	0.000	0.614	−0.003
Sacramento	0.293	0.277	−0.016	0.277	−0.016
<i>Eel River stocks absent from the mixture but present in the baseline</i>					
Coastal ₃	0.000	0.013	0.013	0.000	0.000
Eel	0.000	0.030	0.030	0.009	0.009
Smith	0.000	0.003	0.003	0.100	0.100
Klamath	0.678	0.664	−0.014	0.616	−0.062
Sacramento	0.322	0.291	−0.031	0.275	−0.047
<i>Klamath River stocks absent from the mixture but present in the baseline</i>					
Coastal ₃	0.000	0.049	0.049	0.025	0.025
Eel	0.235	0.169	−0.066	0.133	−0.102
Smith	0.000	0.004	0.004	0.127	0.127
Klamath	0.000	0.087	0.087	0.025	0.025
Sacramento	0.765	0.691	−0.074	0.690	−0.075

TABLE 8. Results of the blind test of GSI with the set of 34 loci used to form stock groups. Estimated standard deviations (SD) accompany stock group contribution estimates.

Stock group	Actual contribution	Pooling procedure			
		Allocate and sum		Pool and allocate	
		Estimate ($\pm$ SD)	Error	Estimate ($\pm$ SD)	Error
Sacramento	0.223	0.272 ($\pm$ 0.057)	0.049	0.242 ($\pm$ 0.026)	0.019
Coastal	0.036	0.028 ($\pm$ 0.086)	-0.008	0.021 ($\pm$ 0.014)	-0.015
Klamath	0.486	0.503 ($\pm$ 0.066)	0.017	0.542 ($\pm$ 0.058)	0.056
S. Oregon	0.246	0.198 ($\pm$ 0.140)	-0.048	0.195 ($\pm$ 0.033)	-0.061
Mid-Oregon	0.009	0.000 ($\pm$ 0.034)	-0.009	0.000 ($\pm$ 0.027)	-0.009

overestimated, and these results show that the allocate and sum procedure can exaggerate this overestimation. These results also show that the trade-off between total estimation error and accurate estimation of a single stock group contribution depends on the particular stock group of concern.

A Blind Test of GSI

The tests using the 1986 CWT data suggested that the GSI method was limited by the degree of concordance between stocks present in the baseline data and the mixture sample and by the number of variable loci available for mixture analyses. To increase the number of available loci, baseline samples were collected again in 1987 and 1988. This resampling more than doubled the number of loci available for mixture analyses. A blind test of the GSI method was then conducted using the 1988 CWT sample to gauge the performance of this new baseline data. To ensure the integrity of the test, the contribution estimates were computed without any prior knowledge of the sample's composition, which was known only to personnel at CDFG.

To summarize the estimation results, five genetic stock groups were defined (Gall et al. 1989) based on a dendrogram of genetic similarity (Wood 1989). The dendrogram was produced using Nei's genetic distance measure (Nei 1972) calculated from the allele frequency estimates for 34 loci in the 35-locus loci set (Table 1), excluding MDHp-2. The MDHp-2 locus was excluded from the construction of the dendrogram because heterozygotes could not be scored directly so that allele frequencies for the jMDHp-2 locus could only be estimated from homozygote frequencies (see Gall et al. 1989 for details). The five prominent genetic stock groups present in the dendrogram were (1) the *Sacramento group* (Coleman Hatchery, Feather River Hatchery, Upper Sacramento River, Merced River Hatchery, and Nimbus Hatchery); (2) the *California coastal group* (Middle Fork Eel River, South Fork Eel River, Salmon Creek, Redwood Creek (on Eel River), Hollow Tree Creek, Van Duzen River, Mad River Hatchery, North Fork Mad River, Mattole River, Redwood Creek, and Redwood Creek Lagoon); (3) the *Klamath group* (Salmon River, Irongate Hatchery, Bogus Creek, Camp Creek, Horse Linto Creek, Shasta River, Trinity River Hatchery, and the South Fork Trinity River); (4) the *Southern Oregon coastal and Smith River group* (Blue Creek, Omagar Creek, Rowdy Creek Hatchery, Middle Fork Smith River, Chetco River Hatchery, Rogue River, Applegate River, and Rock Creek Hatchery); and (5) the *Mid-Oregon coastal group* (Millacoma River, Morgan Creek Hatchery, Fall Creek Hatchery, Elk River Hatchery, and the South Fork Coquille River).

Both the allocate and sum and the pool and allocate procedures were employed to summarize the stock group estimates

TABLE 9. Results of the blind test of GSI using the 35-locus set of loci. Estimated standard deviations (SD) accompany stock group contribution estimates.

Using the allocate and sum procedure			
Stock group	Actual contribution	Estimate ($\pm$ SD)	Error
Sacramento	0.223	0.246 ($\pm$ 0.162)	0.024
Coastal	0.036	0.048 ($\pm$ 0.079)	0.012
Klamath	0.486	0.498 ($\pm$ 0.050)	0.012
S. Oregon	0.246	0.208 ($\pm$ 0.124)	-0.038
Mid-Oregon	0.009	0.000 ($\pm$ 0.131)	-0.009
Using the pool and allocate procedure			
Sacramento ^a	0.219	0.242 ($\pm$ 0.028)	0.023
Coastal	0.037	0.038 ($\pm$ 0.021)	0.001
Klamath	0.489	0.485 ($\pm$ 0.051)	-0.004
S. Oregon	0.247	0.236 ($\pm$ 0.037)	-0.011
Mid-Oregon	0.009	0.000 ($\pm$ 0.031)	-0.009

^aOne sample from the Sacramento stock group had an improbable genotype relative to this baseline data and set of loci.

(Table 8). Mixture analyses were performed with the set of 34 loci used to construct the dendrogram and with the entire 35-locus set of loci (Tables 8 and 9). Data for the MDHp-2 locus were included to see how this affected the accuracy and precision of the estimates (Table 9). Since the MDHp-2 locus was known to be highly variable for the Klamath stocks, variable in some coastal Oregon stocks, and almost monomorphic in other baseline stocks (Gall et al. 1989), it was expected that the use of 35-locus set of loci would improve the accuracy and precision of estimates for the Klamath and possibly other stock groups.

Indeed this was the case, for estimates of the Klamath stock group contribution were more accurate and precise when the 35-locus set of loci was used (Tables 8 and 9). Total estimation errors were also lower for both summarizing procedures when the 35-locus set of loci was used. Further, when the pool and allocate procedure was used with the 35-locus set of loci (Table 9), we estimated that the Sacramento stock group contributed $24.2 \pm 2.8\%$ of the fish (actual 21.9%), the California coastal stock group contributed $3.7 \pm 2.1\%$ (actual 3.7%), the Klamath stock group contributed $48.5 \pm 5.1\%$ (actual 48.9%), the Southern Oregon coastal and Smith River stock group contributed $23.6 \pm 3.7\%$ (actual 24.7%), and that the Mid-Oregon coastal stock group contributed $0.0 \pm 3.1\%$ (actual 0.9%). Thus, we were able to estimate very accurately the contributions of five major stock groups to the mixture sample.

Discussion

The results of the blind test show that GSI analysis can produce accurate stock group contribution estimates using actual fishery data collected in ports along the Oregon and California coasts. With the number of polymorphic loci available for analysis of chinook salmon and appropriate baseline data, the estimated contributions of stock groups to the mixture sample had absolute errors no greater than 6.2% and had total estimation errors no greater than 16.0%. In addition, the blind test results compared favorably with other test results, despite the fact that the blind test was performed on the smallest mixture sample used in this study. Indeed, with 35 loci using pool and allocate, the estimation error for each stock group was less than 2.3% based on a sample of only 220 fish.

The results of the blind test also corroborate the validation study of Milner et al. (1981) (performed on mixtures composed of tagged juvenile fish) as well as the findings of several simulation studies showing that the GSI method can produce accurate results using genetic data for Pacific salmon (Fournier et al. 1984; Beacham et al. 1985; Pella and Milner 1987; Wood et al. 1987; Brodziak 1990). In particular, the blind test results are consistent with the findings of Wood et al. (1987, fig. 9) that show that small mixture samples are sufficient for mixture analyses when enough genetic variability exists between stock groups. While simulation studies are an extremely useful tool to examine the sensitivity of the GSI method to various assumptions, such studies cannot anticipate some difficulties that can occur in practice, even when resampling techniques such as the bootstrap are applied to simulate the effect of sampling variation. Indeed, the difficulties with the LDH-C locus that occurred during our preliminary analyses using the 1986 CWT sample show the importance of proper handling of tissue samples, data standards, and thorough screening of all variable loci to the GSI method. Spurious genetic variation was observed in the 1986 CWT sample at the LDH-C locus because some tissue samples were not stored in -80°C freezers. Electrophoresis of the LDH enzyme using the degraded tissues produced misleading banding patterns. Thus, tissue degradation altered data interpretation, which in turn led to inaccurate stock composition estimates. At present, GSI laboratories at UCD, Washington Department of Fisheries, and NMFS have exchanged standards and tissue samples to assure consistent allele scoring for chinook salmon. In fact, the LDH-C*70 allele was eliminated from the coast-wide database for chinook salmon in 1989 because this allele was determined to be an artifact of poor sample quality. At present, there is also an interlaboratory loci sponsorship program that excludes a locus from the coast-wide baseline if any of the participating laboratories cannot reliably score the alleles for that locus. Such cooperation has greatly enhanced and accelerated the advancement of GSI technology for fisheries management. Additionally, many loci now recognized as important for GSI analyses of chinook salmon were not available for the preliminary analyses or tests using the 1986 CWT sample because of primitive laboratory techniques that impaired the detection of variable loci.

Nonetheless, the tests using the 1986 CWT sample lead to a number of observations that have broader implications to the general application of the GSI method. First, the results of the tests on the effect of choosing stocks included in the baseline data show that the magnitude of estimation error for a particular stock group depends on which stock groups are included in the baseline, if the set of loci and mixture sample are fixed. Accurate estimates for the targeted Eel and Smith stock groups were

accompanied by inaccurate estimates for the Klamath and Sacramento stock groups. On the one hand, by including as many source stocks and loci as possible, substantial misallocations to noncontributing stocks can occur. On the other hand, estimation errors can also be substantial if contributing source stocks are excluded based on prior assumptions about fishery composition. Both situations are undesirable. However, a lack of detectable genetic differences between stocks may preclude accurate estimation even if the baseline data can be judiciously chosen to exclude stocks whose contribution to the mixture sample is insignificant. This highlights the need to examine existing data and hypotheses concerning the mixing and relative abundance of stocks when testing the adequacy of baseline data. Such tests can be performed using a combination of validation studies and exploratory simulation and genetic similarity analyses (Wood et al. 1987; Wood et al. 1989) before a final selection of stocks to include in the baseline data is made.

The results of the test comparing the 11-locus and 15-locus sets of loci show that changing the loci used in the analysis may improve estimation accuracy for some stock groups and simultaneously decrease the estimation accuracy for others. In particular, with the four additional loci the overestimate of the Redwood Creek stock group increased by 1%, while the estimation errors for the Eel, Klamath, and Sacramento stock groups decreased by less than 2%. In general, adding more loci will cost more money, but might not appreciably improve estimation accuracy for important stock groups. On the other hand, the blind test results show how the addition of a single variable locus can increase the accuracy of the estimates. In principle, loci should be selected to decrease estimation error, and their relative effect on estimation error should be quantified before the GSI method is applied (cf. Gomulkiewicz et al. 1990).

The results of the test on the effect of stock grouping on the pool and allocate procedure show that enlarging the number of groups can decrease estimation accuracy for the pool and allocate procedure for a fixed mixture sample and set of loci. In fact, the lowest maximum absolute error was obtained using three stock groups at the expense of combining the Eel and Smith contributions. Creating two additional stock groups by splitting up the Coastal₅ group increased estimation errors for the Eel, Klamath, Sacramento, and Smith groups. However, progressing from five to seven stock groups did not appreciably affect the results and increased the largest absolute error by only 1%. Although the contributions of the three additional stock groups (Mad and Mattole rivers and Redwood Creek) were estimated accurately with seven groups, their summed estimation error was 3.9% larger when they were combined as a single unit ("Coastal₃" group). Thus, the choice of the best level of stock grouping depends on the accuracy required for each group's contribution.

Overall, the definition of stock groups should reflect the relative degree of genetic similarity among stocks within the baseline data to reduce misallocation to noncontributing stocks that exhibit genetic affinity with contributing stocks. Genetic similarity analyses can be useful for defining stock groups (Wood et al. 1989), but for stocks originating in northern California coastal rivers, the resulting groups might conflict with management programs that use geographic proximity to group stocks (Gall et al. 1989). In particular, by using seven instead of three stock groups, the assumption of independence of stock groups required by the standard GSI model may be untenable given the amount of detectable genetic variation. Such attempts to obtain more information from a limited set of genetic data may decrease estimation accuracy. This underscores the point

that attempting to accurately estimate the contribution of a particular stock group may be limited by genetic similarity between stocks.

The results of the test comparing the allocate and sum and the pool and allocate procedures show that the choice of a summarizing procedure may be important to the accurate estimation of particular stock group contributions. However, under the best circumstances, the estimation errors for all stock groups were small (less than 2%) using either the allocate and sum or the pool and allocate procedure. Thus, the summarizing procedure does not always affect the accuracy of the estimation.

Similarly, the absence of the Eel and Klamath stock groups was detectable by both summarizing procedures, if one accepts relatively small contribution estimates to indicate absence. However, while the pool and allocate procedure more accurately detected the absence of the targeted stock group in this test, it also increased the error for the nontargeted stock groups. The application of a variant of the standard GSI model to detect the number of source stocks present in the mixture might be helpful when the detection of an individual stock or stock group is important (Smouse et al. 1990).

A comparison of the results of Tests 2 and 3 also shows that the allocate and sum procedure can dominate the pool and allocate procedure with respect to total estimation error. In addition, a comparison of the precision of the two summarizing procedures in the blind test shows that, for these data, the pool and allocate procedure produces variance estimates for stock group contributions that are smaller than those using the allocate and sum procedure. So, although the allocate and sum procedure is more flexible and easier to apply to summarize contribution estimates (Wood et al. 1987), direct comparisons of the performance of the procedures should be made before the decision to apply either is made. These comparisons can be explored using validation or simulation studies.

GSI has emerged as a powerful tool in fisheries management (Shaklee et al. 1990b; Waples et al. 1990), and we have demonstrated that GSI has tremendous potential application to accurately assess the composition of chinook salmon fisheries off the coasts of California and Oregon. Regardless of the particular application, fisheries managers who want to use GSI to analyze the composition of mixed-stock fisheries must make practical choices in the face of the uncertain, but potentially important, effects of manipulating the genetic data. In general, the loci used for mixture analyses should reflect both the cost limitations of management programs and the accuracy requirements for improving the quality of stock assessments. However, the manipulation of baseline data to reflect groupings of stocks into management units may preclude the possibility of accurately estimating some stock groups' contributions. In such cases, the use of other population characteristics may improve the discriminatory power of stock identification analyses (Fournier et al. 1984; Wood et al. 1989). Moreover, even with prior information about the composition of a mixed-stock fishery, it is recommended that the adequacy of baseline data be examined through validation and simulation studies before GSI analyses are used to provide stock assessment advice. Nonetheless, our results are further evidence that GSI can provide accurate estimates of stock contributions in mixed-stock fisheries when the method is carefully applied.

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Appendix

TABLE A.1. Summary of stock groupings and stocks of origin for all chinook salmon in the 1986 CWT sample.

Stock group	Stock of origin	Sample size (percentage of total)
Sacramento	Coleman Hatchery	64 (3.9%)
	Feather River	80 (4.9%)
	Merced River	67 (4.1%)
	Mokelumne River	3 (0.2%)
	Nimbus Hatchery	50 (3.1%)
	Tehama Colusa	1 (0.1%)
Middle coast	Yuba River	5 (0.3%)
	Eel River	1 (0.1%)
	Redwood Creek (on Eel River) ^a	18 (1.1%)
	Silverado ^a	33 (2.0%)
	Silverking ^a	1 (0.1%)
	Sprowel Creek ^a	4 (0.2%)
North coast	Van Arsdale ^a	26 (1.6%)
	Bogus Creek ^b	4 (0.2%)
	Iron Gate Hatchery ^b	115 (7.1%)
Oregon coast	Trinity River ^b	454 (27.9%)
	Anadromous Inc.	123 (7.6%)
	Butte Falls	5 (0.3%)
	Cole Rivers	293 (18.0%)
	Elk River	50 (3.1%)
	Oregon Pacific	25 (1.5%)
	Oregon Aqua Foods	35 (2.2%)
	Rock Creek	32 (2.0%)
	Rogue River	40 (2.5%)
	Salmon River	4 (0.2%)
	Stayton Pond	2 (0.1%)
Columbia River	Trask River	43 (2.6%)
	Bonneville	3 (0.2%)
	Cowlitz	13 (0.8%)
	Hagerman	2 (0.1%)
	Lewis River	1 (0.1%)
	Little White Salmon	1 (0.1%)
	Lyons Ferry	12 (0.7%)
	McNary	1 (0.1%)
	Priest Rapids	1 (0.1%)
	Rocky Reach	8 (0.5%)
	Spring Creek	1 (0.1%)
Washington coast	Washougal	6 (0.4%)
	Nemah	1 (0.1%)
	Quinault	1 (0.1%)

^aSamples originating in the Eel River drainage (see Test 4).

^bSamples originating in the Klamath River drainage (see Test 4).

LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on Mortality Rates of Dungeness Crabs (*Cancer magister*)

Smith and Jamieson (1989b) published recently in this journal on natural and fishery mortality rates of male Dungeness crabs, *C. magister*, near Tofino on the west coast of Vancouver Island from 1985 to 1987. Based on analyses of tag-recovery data, these authors reported that sublegal male crabs (<154 mm notch-to-notch carapace width, CW) experienced very high natural mortality rates (annual $M = 2.9$ – 4.5) and that legal males were subject to extremely high fishing mortality rates (annual $F = 5.1$ – 6.9). Given these estimated instantaneous mortality rates, minimum annual mortality rates (A) of sublegal and legal male crabs would be 0.94 and 0.99, respectively. These extremely high mortality rates led Smith and Jamieson to argue for continuous (year-round) fishing and to question “the appropriateness of the current minimum legal size limit of 165 mm spine-to-spine carapace width (British Columbia) for achieving optimal levels of yield- and eggs-per-recruit.”

Smith and Jamieson’s estimates of instantaneous fishing mortality rates (annual F) greatly exceed those which we recalculate from Gotshall (1978: $F = 1.00$ – 2.06) and Methot and Botsford (1982: $F = 0.56$ – 2.03) for the northern California Dungeness crab fishery (1966–1967 and 1971–72 seasons for which both papers present comparable estimates). (This fishery is open from December through July, but Smith and Jamieson appear to have assumed a year-round fishery.) Smith and Jamieson’s estimates of natural mortality rates (annual M) greatly exceed those reported for the crab *Scylla serrata* (Hill 1975: $M = 0.53$ and $M = 0.92$ for 2- and 3-yr-old crabs respectively) and are a priori implausible. Finally, if one uses Hoenig’s (1983) combined predictive regression equation to estimate M from maximum longevity (assumed to be 8 yr: Butler 1961), the predicted value of M is 0.55.

Because estimates of mortality rates have important implications for fishery management policy, we present in this comment a brief critique of methods that Smith and Jamieson used to arrive at their estimates. We begin our critique with a brief description of the release and recovery data relied upon by them, and we review the methods that they used to calculate mortality rates. We follow this by a discussion of several serious flaws in their use of these data. We then present alternative estimates of mortality rates based on maximum longevity (Hoenig 1983) as well as our own “best guess” of mortality rates for male Dungeness crabs. We conclude with a few general remarks. Our critique shows that Smith and Jamieson reported unreliable and positively biased estimates of mortality rates that are unrealistically high.

Description of tag releases and recoveries, and methods of analysis

Smith and Jamieson failed to give clear specifications of the total number of crabs tagged, size and shell condition at tagging, and the dates on which crabs were tagged. From the totals in their table 2 and the caption to their fig. 4, it appears that 3589 sublegal male crabs ranging from 125 to 155 mm CW

were tagged. Their caption to fig. 1 states that “most tagging was done from May–July 1985,” but their text indicates that crabs were “trap caught, tagged, and released between April 1985 and May 1986,” and their fig. 4A suggests that about 50% of all sublegal crabs, and perhaps 75% of those 125–140 mm CW, were tagged during January–May 1986. Their fig. 4 also suggests that recoveries (at least as legal-sized crabs) were received from August 1985 through February 1987. No data on shell condition at time of tagging were given. Crabs were tagged with blue (FLOY) T-bar anchor tags. They cite no other reference where tagging data are presented clearly.

Tag recoveries in Smith and Jamieson’s research apparently originated from three distinct sources: (a) four “special fishermen” who recorded tag numbers on special recovery forms; (b) other fishermen who tended not to report recoveries of sublegal male crabs, but who did report recoveries of legal crabs; and (c) research traps, which consisted of three types with different size-selective properties. In their analysis of recovery data, data from all three sources were combined.

Smith and Jamieson placed substantial reliance on analysis of the declines in $\ln$ number of recoveries with time-at-large among crabs tagged and recovered as sublegals (their fig. 1), or tagged and recovered as legal (their fig. 2). For example, they fit a linear regression line to $\ln$ sublegal recoveries versus time-at-large (for crabs tagged at sublegal sizes), from which they obtained an estimated slope (in days) of 0.00954. They then converted this daily slope to a maximum estimate of (annual) M of 3.5 (95% C.I. for slope was 2.9–4.1). They also placed substantial reliance on recovery data for crabs tagged when of sublegal size but recovered at legal size. These data were adjusted for “compliance rate” (tag reporting rate) and for size-dependent probabilities of reaching legal size within the period of recovery (see caption to their table 2) to produce estimates of M for individual CW intervals. These estimates ranged from about $M = 2.9$ to $M = 4.4$ and generally increased with increasing CW.

Flaws in use and analysis of recovery data

Chief among our concerns with Smith and Jamieson’s use and analysis of their recovery data are the following: (a) combination of recovery data from several sources; (b) nonconstancy of fishing effort; (c) confounding of natural mortality with molting to legal size; and (d) unknown shell condition of tagged crabs.

Combination of recovery data — Smith and Jamieson did not justify their combination of recovery data from several different sources, and we believe that this combination was flawed for several reasons. First and most importantly, size-specific recovery rates could not have been the same in the three different types of “gear” used for recovery. As the authors pointed out, their research traps had modified escape ports or lacked such escape ports, and the four “special fishermen” reported recoveries of sublegal crabs whereas other fishermen apparently did not or did so at a much lower reporting rate. Thus, each “gear type” must have had different size-selective properties with respect to tagged crabs. Second, each recovery “gear type” could not have been fished with the same relative inten-

sity over time. For example, it seems likely that Smith and Jamieson used their research traps with greatest effort during the May–August 1985 and January–May 1986 tagging periods. Also, the four “special fishermen” must have accounted for a time-varying proportion of total fishing effort. Third, the authors do not state whether or not all recovered tags were removed from the tagged population or were instead returned.

Together, the above observations suggest that meaningful analysis of combined recovery data is not possible because any declines or changes in recovery rates with time would be confounded by varying intensity of recovery effort and selectivity with time. This problem is especially acute when research traps are designed to retain small crabs that are not retained in commercial traps. Therefore, Hankin et al. (1989) released all tagged crabs which were recovered in their research traps and did not count these among their recoveries. If Smith and Jamieson’s research traps were fished most intensely during periods of tagging, then combining all recovery data probably resulted in substantial positive bias in estimation of M .

Nonconstancy of fishing effort — When total instantaneous mortality rate (Z) is estimated by regressing $\ln$ recoveries against days-at-large, the critical assumption is that fishing effort (F) and natural mortality rate (M) remain reasonably constant over the recovery period. We contend that this assumption was clearly violated for Smith and Jamieson’s recovery data, and we provide a summary of monthly fishing effort (days) during 1985 and 1986 in the Tofino (Area 24) fishery (DFO 1986–87) in support of this contention:

Year	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
1985	64	60	68	116	176	168	149	122	92	134	149	93
1986	69	80	105	362	370	284	434	305	318	512	323	186

Although fishing took place during all months, effort data provide clear evidence of a seasonal (April–November) fishery which would produce large seasonal fluctuations in F . Note, however, that the above fishing effort data do not reflect total recovery effort which was augmented by the four “special fishermen” and research traps to an unknown degree.

In Smith and Jamieson’s research, their use of the above regression procedure to estimate mortality rates is further complicated by their tagging of two “groups” of crabs during two major periods: May–July 1985 and January–May 1986. Since $\ln$ recoveries were plotted against days-at-large, regardless of date of release, one must further assume that each tag group was exposed to identical mortality rates following their release. Interannual variation in fishing effort, of course, makes it extremely unlikely that this assumption would ever be met. Indeed, the coefficient of variation of total annual fishing effort at Tofino was nearly 60% for the period 1978–89 (DFO catch statistics).

The authors calculated $Z = 9.2$ for legal males from their fig. 2 by multiplying the daily (negative) slope of the regression line, 0.0253, by 365 d, thereby assuming that the rate found over approximately 6 mo remained constant throughout the year. These legal-sized crabs were tagged “mostly in spring 1986” and would have been exposed to the months of greatest fishing effort over the following 6 mo. Their extrapolation of slope would therefore result in substantial positive bias in estimation of annual Z .

Confounding of natural mortality with molting to legal size

Smith and Jamieson used a regression of $\ln$ recoveries against days-at-large for crabs tagged and recovered at sublegal sizes to generate a “maximum” estimate of annual $M = 3.5$ with a 95% C.I. of 2.9–4.1 (their fig. 1). Their table 2 gives final estimates of M , however, which ranged from 2.9 to 4.4 for sublegal crabs, essentially spanning the same 95% confidence interval of slope for annual M . The slope of this regression line would give an unreliable and positively biased estimate of M because losses to the tagged population of sublegal crabs are not restricted to natural mortality. Instead, crabs could be lost to the tagged population of sublegal crabs because they molted to legal size or suffered fishery-related handling mortality (see next section). (Although crabs could also lose tags if they molted, we agree with Smith and Jamieson that such loss would likely be small.)

According to their fig. 4, 76.5% of the crabs tagged as sublegals were in the size range 140–155 mm CW; of these, about 40% appear to have been tagged during May 1985. For any of these crabs that were tagged in a hard-shelled condition, molting would have taken place within no more than 2 or 3 mo, and virtually all of these crabs would have exceeded legal size after molting (see caption to their table 2). In the 1986 tagging period, fewer crabs in this size range were tagged, but all tagging appears to have been completed by the end of March. All of these crabs would therefore have been expected to molt to legal size during the following spring/summer molting season. Published studies of growth of male Dungeness crabs (e.g. Butler 1961; Lehman and Osborn 1973; Warner 1987) suggest that annual molting probabilities must be close to 1 for crabs below legal size. Given this information, a significant statistical decline in recoveries of sublegal crabs with days-at-large would have been expected even if all sublegal tagged crabs had survived. Natural mortality and molting to legal size were seriously confounded, and a regression of $\ln$ recoveries against days-at-large could therefore not produce a meaningful estimate of M .

Uncertain shell condition of tagged crabs — Although Smith and Jamieson (1989b) did not provide data concerning shell condition of tagged crabs, their paper does suggest that substantial numbers of soft-shelled crabs were tagged and released. Approximately half of their crabs were tagged from May through July 1985 (Smith and Jamieson 1989b, fig. 4), and they stated (p. 1612) that about 50% of legal males in the commercial catch were soft-shelled during the peak molting season (spring/summer).

Based on laboratory mortality rates among crabs held after tagging, Smith and Jamieson discounted “tagging-induced” mortality. Earlier workers (Cleaver 1949; Waldron 1958), however, reported that recovery rates of tagged soft-shelled *C. magister* were less than those of tagged hard-shelled *C. magister*. For example, Cleaver (1949) found in 1948 that, compared with crabs tagged having “new, hard” shells, those with “new, slightly soft” shells and others with “new, soft” shells had 8.1 and 68.5% fewer returns, respectively. Reanalysis of Waldron’s (1958) data also suggests a significant difference in return rates between crabs tagged with “carapace very rigid” and those tagged with the carapace “slightly to moderately flexible” ($\chi^2 = 50.17$, $P < 0.01$, calculated from his table 3). Cleaver (1949) and Waldron (1958) used Peterson disc tags, fastened near the large lateral carapace spine, whereas Smith and Jamieson adopted the newer T-bar anchor tags, inserted at the posterior epimeral line. Nevertheless, in the

absence of contrary evidence for the anchor tags, we believe it reasonable to question the latter authors' acceptance of minimal tagging mortality.

We suspect that tagging mortality of soft-shelled crabs may have been very substantial, especially among crabs tagged from 145 to 155 CW. Table 2 of their paper shows that their recovery rates of legal crabs from those tagged at sizes from 145 to 155 mm CW were much lower ($53/2246 = 2.4\%$) than those for crabs tagged at sizes from 125 to 145 mm CW ($112/1343 = 11.7\%$). As mentioned above, virtually all of those crabs tagged at sizes exceeding 145 mm would be expected to exceed legal size after a single molt. In contrast, as stated by Smith and Jamieson, for crabs in the "intervals, 125–130- and 130–135-mm CW. . . only 50 and 90% of crabs this size are expected to attain legal size with their next moult." Two (annual) molts would have been required for many of these smaller crabs to reach legal size, and tag loss through two molts (as opposed to one molt) is probably large. Thus, a much greater fraction of crabs tagged in the smaller size interval (125–145 mm at tagging) were recovered at legal size, even though size-specific molt increments would greatly favor recovery of sublegal crabs tagged at the larger sizes (145–155 mm).

Possible causes for the differential recovery rates reported in their table 2 include size-dependent differences in (a) tagging mortality of soft-shelled individuals; (b) trapping and handling mortality; (c) annual molting probabilities; or (d) tag reporting rate. As previously mentioned, we find no literature support for a substantial decline in annual molting probabilities among male crabs with premolt CW < 155 mm. Although fishermen may have captured and sold sublegal tagged crabs > 150 mm CW and failed to report this illegal practice, we have no evidence in support of this possibility.

Figure 4 of Smith and Jamieson's paper indicates that most crabs in the 140–155 mm CW interval were tagged during May–July 1985 at the probable peak of the molting season. Very few crabs in the 125–140 mm CW interval were tagged that year. Tagging in 1986, including tagging of almost all crabs in the 125–140 mm CW interval, took place primarily during January–March during which time almost all crabs should have been hard-shelled. There is thus circumstantial evidence in support of a contention that a much greater proportion of crabs in the larger size interval were tagged in a soft-shelled condition. The observed discrepancy in size-specific recovery rates is consistent with differential tagging mortality between crabs tagged with soft or hard shells.

Smith and Jamieson described the trapping and handling of soft crabs as an "important contributor" to crab mortality, and here we agree. We note, however, that crabs in the 125–145 mm CW interval should be less vulnerable to such mortality because these smaller crabs have a lower retention rate in commercial crab traps (Smith and Jamieson 1989a). Thus, among sublegal tagged crabs in soft-shelled condition, handling mortality due to repeated fishery capture and release would be greater for crabs 145–155 mm CW.

Estimation of "compliance rate" — Smith and Jamieson reported (p. 1611) that 182 legal males were recovered of 341 released, giving a recovery rate of 0.534. This recovery rate provides a valid minimum estimate of exploitation rate because $182 = \lambda \cdot E \cdot 341$, where λ = tag reporting rate ($0 \leq \lambda \leq 1$) and E = exploitation rate ($0 \leq E \leq 1$). (The rate 0.534 is also a valid minimum estimate of tag reporting rate because a value lower than that would produce an impossible exploitation rate in excess of 100%).

Using basic mortality equations relating E to F and Z , and with their annualized estimate of $Z = 9.2$, we have for legal-sized crabs

$$0.5434 = \lambda \cdot E = \lambda \cdot F(1 - e^{-Z})/Z$$

so that

$$\lambda \cdot F = 0.534 \cdot 9.2 / (1 - 0.0101) = 4.913.$$

(Note that we use these values of E and Z for illustrative purposes only, having previously argued that the above estimate of Z must be positively biased.) For a tag reporting rate of 100%, F will take on its minimum value of 4.913 whereas corresponding F 's for tag reporting rates of 90, 80, 70, and 60% would be 5.46, 6.14, 7.02, and 8.19, respectively. Corresponding M 's, given $Z = 9.2$, are 3.74, 3.06, 2.18, and 1.01, respectively. These calculations demonstrate the importance of knowing the true tag reporting rate for separation of Z into its components, F and M .

As the above simple algebra illustrates, however, λ and E are confounded in tag recovery data and there is, in general, no nice method for their separation when there is only a single release of animals with the same tags. Although we could not follow the logic of the methods used by Smith and Jamieson to revise their estimate of reporting rate (p. 1611) upwards to 87%, we accept that value as a reasonable one.

Alternative estimates of mortality rates

Hoening (1983) developed regression equations to predict M of fish and cetacean and molluscan stocks from maximum ages. We used his "combined" equation (for all taxonomic groups)

$$\ln M = 1.44 + (-0.982) \ln t_{\max}$$

and we let $t_{\max}$ range from 5 through 8 yr. Predicted values of M and of the conditional annual mortality rates ($n = 1 - e^{-M}$) are listed below:

$t_{\max}$	M	n
5	0.87	0.58
6	0.73	0.52
7	0.62	0.46
8	0.55	0.42

Hoening's (1983) method probably produces predictions of M that are less than those actually experienced by Dungeness crabs because fish, cetaceans, and molluscs do not experience molting-related mortality. We believe, however, that these values present useful lower bounds for natural mortality rates of Dungeness crabs. As argued above, there are strong reasons to believe that Smith and Jamieson's estimates of M (from release and recovery of sublegal crabs) and Z (from release and recovery of legal crabs) have serious positive bias and must be regarded as implausibly high.

Published literature estimates of natural mortality rates of crabs include Hill's (1975) estimates for *S. serrata* ($M = 0.53$ and 0.92 for 2- and 3-yr-old crabs) and Hankin et al.'s. (1989) estimates for female Dungeness crabs exceeding 155 mm CW ($M = 1.9$ and 2.6 during two different years). Hankin et al. (1989) believed that these high mortality rates reflected senescence among these largest female crabs, and they noted that estimates may have been positively biased due to tag loss and fishery handling mortality. Hankin et al.'s (1989) tag recovery data for smaller female Dungeness crabs could not be used to estimate mortality rates, but these data were clearly not com-

patible with the high natural mortality rates estimated for larger females. It seems very unlikely that M exceeds 1.2 for these younger crabs, and it is possible that M is substantially less. Apart from the preceding examples, we have been unable to find other published estimates of natural mortality rates for crabs. We provisionally conclude that natural mortality rates for male Dungeness crabs may lie in the range $0.8 < M < 1.2$, although lower values seem quite plausible.

It is generally accepted that annual exploitation rates for Dungeness crabs range from 60 to 90%. The table below list values of annual fishing mortality rate, F , for various combinations of E and M restricted to the range 0.8–1.2:

Natural mortality rate, M

Exploitation rate, E	0.80	1.00	1.20
0.60	1.58	1.79	2.02
0.70	2.24	2.59	2.97
0.80	3.46	4.14	4.87
0.90	7.24	9.02	10.82

Using Smith and Jamieson's recovery data for legal-sized crabs and their compliance rate estimate of 87%, the exploitation rate in the Tofino fishery during 1986 was approximately 61%. From the above table, it is evident that the range of F reported in their paper, $F = 5.1$ – 6.9 , is implausibly high for the 1986 Tofino fishery. It appears possible that F 's of this magnitude can indeed be realized in Dungeness crab fisheries, however.

Concluding remarks

We believe that the extremely high natural and fishery mortality rates reported by Smith and Jamieson have serious positive bias, and we object to their application of these estimates to important management questions such as soft-shell seasons and size limits. There is, however, value in their paper in that it has brought to light a possibly large fishery-related mortality in the Tofino operation. Although Smith and Jamieson's data cannot produce reliable estimates of mortality rates, their data provide circumstantial evidence that repeated capture and release of soft-shelled sublegal males may cause substantial fishery-related mortality. An area or time period closure to protect soft-shelled crabs would help to ensure that most fishery-related mortality is due to capture of legal males that produce economic benefit. Currently, according to Smith and Jamieson, "new markets for soft-shelled males have resulted in many fishermen reluctantly retaining them in order to remain competitive." Ex-vessel price per pound for these soft-shelled males appears to be less than one third that of hard-shelled males — T. H. Butler, *Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada*, and D. G. Hankin, *Department of Fisheries, Humboldt State University, Arcata, CA 95521, USA*. (JB357)

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Reply to Butler and Hankin: Mortality Rates of Dungeness Crabs (*Cancer magister*)

We were not particularly surprised that our unusually high estimates of natural ($M = 2.9$ – 4.5) and fishing ($F = 5.1$ – 6.9) mortality for Dungeness crabs (*Cancer magister*) near Tofino, British Columbia (Smith and Jamieson 1989b), have caused others to doubt them. We ourselves were skeptical of the estimates obtained from the analysis of the data we had collected over the 18-mo period of our study. This skepticism prompted us to further analyze our data for other possible sources of tag disappearance. We therefore revised our estimate of natural mortality to $M = 2.3$ – 2.8 (Smith and Jamieson 1990). This more recent analysis accounted for the possibility of movement out of the study area, or into areas of relatively low fishing intensity (Ricker 1975), where they would be less likely to be recaptured.

We, as well as anyone else who has relied on mark–recapture data, are fully aware of the limitations of the methodology. We also realize that mortality rates can vary within and among habitats, over time, in relation to population and predator and prey densities, and in relation to environmental factors. However, we will defend criticism that our analyses have presented implausible and unreliable estimates of Dungeness crab mortality near Tofino, B.C., during the period of our study. We will attempt to convince readers that the fishing and mortality rates of Dungeness crabs reported in Smith and Jamieson (1989b) were based on a competent treatment of the data. We will reiterate that fishing mortality of male Dungeness crabs during our study was likely much higher than one might presume prior to careful study of this intensely fished population.

Before addressing the specific criticisms by Butler and Hankin, we wish to point out that, according to the first few paragraphs of their critique, their motivation for criticizing our work is a concern that we might be inappropriately recommending management options based on our results. This is not true. A reading of Smith and Jamieson (1989b), in particular the discussion, will show that we did not argue for year-round fishing. We did not argue for or against anything, but we do feel it is appropriate to draw attention to current management practices when new information of Dungeness crab population dynamics becomes available for consideration and debate. Important studies of Dungeness crab dynamics off northern California assumed mortality rates dramatically less than we obtained in our study near Tofino (Botsford and Wickham 1978; McKelvey et al. 1980).

Butler and Hankin correctly point out our error in assuming a year-round fishery in our comparison of our results with those of Gotshall (1978) and Methot and Botsford (1982). Gotshall's (1978) estimates of F during the fishing season ranged from 0.7 to 5 from 1966–67 until 1971–72, while Methot's and Botsford's (1982) estimates for northern and central California ranged from 0.6 to 3.2 during the fishing season for 1951–52 until 1976–77. Gotshall (1978) estimated M to be as high as 1.78 during his 1966–67/1971–72 study, but we acknowledge unacceptable uncertainty in his estimates. Our estimates of natural and fishing mortality for the fishery near Tofino are higher than those obtained by Gotshall (1978) and Methot and Botsford (1982). However, their results are for a relatively unbounded fishery along the open coast of California whereas the fishery in Tofino is local, somewhat geographically bounded, and intensely fished at relatively low investment and operating costs to the participants. The fishing conditions are mostly ideal and require no unusual fishing skills. Most of our study site occurs within eyesight of the town of Tofino.

The proximity of the fishery to fishermen's homes means some fishermen haul their traps as frequently as daily. The fishery near Tofino is highly competitive. When one considers that fishing intensity (Ricker 1975) near Tofino (≈ 5200 trap hauls $\cdot \text{mo}^{-1} \cdot \text{km}^{-2}$ (Smith and Jamieson 1990)) is probably about an order of magnitude greater than off northern California, such an unusually high rate of fishing mortality is not implausible. We arrive at a rough estimate of fishing intensity in northern California of ≈ 500 trap hauls $\cdot \text{mo}^{-1} \cdot \text{km}^{-2}$. This estimate is based on a fishery using $\approx 50\,000$ traps (McKelvey et al. 1980) hauled over an area $\approx 1500 \text{ km}^2$ ($\approx 300 \text{ km}$ of coastline by $\approx 5 \text{ km}$ of shelf (R. Warner, California Department of Fish and Game, Eureka, CA, pers. comm.)) every other day (on average over the fishing season). Exceptionally high fishing mortality of legal-sized male Dungeness crabs is not a novel concept. Others have been led to consider that in some fisheries, virtually all legal males are captured each season (Cleaver 1949; Petersen 1973; Botsford and Wickham 1978).

We will now address the four concerns about our mark-recovery methodology and analysis which Butler and Hankin highlight.

1. Combination of recovery data

Our choice to analyze recovery data from different trap types to measure the rate of disappearance of sublegal-sized crabs would only be a concern if those different trap types had markedly different selectivities for the size of crabs we tagged. In recognition of this potential problem, we defined our sublegal size category in fig. 1 of Smith and Jamieson (1989b) as crabs 145–155 mm notch-to-notch carapace width (CW), eliminating consideration of smaller crabs. Study of the retention probabilities of crabs of different sizes in table 3 in Smith and Jamieson (1989a) shows that for trap types A (our research traps) and B (the commercial trap type in general use) the selectivities for crabs in that size range are similar.

Trap types C and D had the least ability to retain sublegal-sized crabs. Trap type C was not used near Tofino, and trap type D was used by only two fisherman in the region. One of these two fishermen happened to be one of the four "special fishermen" who recorded the recovery of sublegal-sized crabs. These four fishermen, and all others fishing near Tofino, had been instructed to rerelease sublegal-sized males that they had captured. Because of his larger escape ports, the fisherman using trap type D recorded fewer recoveries of sublegal-sized crabs. This was not an important factor in our analyses because,

as we will explain, his fishing effort was relatively constant over time. In preliminary analyses of the recovery data the possibility of bias due to selectivity factors was evaluated and considered uninformative.

Contrary to the assumption of Butler and Hankin, we did not fish our research traps more intensely during the 1985 and 1986 tagging periods. During the period of our study, we were operating on an approximately monthly sampling schedule where we would spend 1 wk in Tofino during which we would haul a more or less constant number of our research traps. On some of these trips, we would be tagging and releasing crabs. However, most tagging was done by B.D.S. onboard commercial vessels. In addition to the week a month during which we hauled research traps, B.D.S. spent about a week in Tofino during which he would sample catch and tag crabs onboard commercial vessels and visit fishermen to obtain effort information.

Overall, we did not vary our research fishing effort markedly over the period of the study. Some extra effort was expended during the summer of 1985 in upper Lemmens Inlet and in the summer of 1986 near Indian Island to perform the experiments described in Smith and Jamieson (1989a). Similarly, the four fishermen who were kind enough to record all recoveries of tagged crabs and release the sublegal-sized crabs for us also did not have particularly variable seasonal fishing effort. The fishery was open year-round and, as previously mentioned, the weather and fishing conditions near Tofino are favourable year-round. The four fishermen who participated closely in our study fished with a relatively steady effort trend over the period of our study. Official landing statistics show a summer increase in fishing effort and landings, but this arises from the entry of many local part-time fishermen into the fishery as well as fishermen from other ports, particularly Vancouver (Smith and Jamieson 1990).

As part of our study, we kept records of our own fishing effort, that of the four fishermen who were particularly helpful, and that of as many others as we could contact. We collected information on the number of traps in the water, the frequency with which they were hauled, and the location they were fished on a biweekly to monthly basis. During preliminary analysis of our recovery data, we used this information but found that seasonal changes in fishing effort had little bearing on our conclusions. To simplify the presentation of our results, we excluded it. We later used this information in a different manner in a simultaneous analysis of movement and mortality of Dungeness crabs near Tofino (Smith and Jamieson 1990) but, as argued here, we did not consider seasonal changes in effort by the four particularly helpful fishermen an important variable. (Note that in Smith and Jamieson (1990), we refer to three, not four, fishermen. Two fishermen shared the same boat but in that paper, we did not acknowledge that fact.)

2. Nonconstancy of fishing effort

Constancy of fishing effort and natural mortality over the recovery period were not critical assumptions in our attempt to estimate total mortality. It was more important that there were no marked trends in either of those two variables over the recovery period. Of these two variables, we think it is reasonable to judge that fishing effort would be more variable. Our calculation of total mortality in fig. 2 of Smith and Jamieson (1989b) depends on the rate of recovery of legal-sized males released in April and May of 1986. These crabs were subsequently recovered over the next approximately 6 mo.

Regression analysis on the 1986 effort data for Canadian Department of Fisheries and Oceans Statistical Area 24 pre-

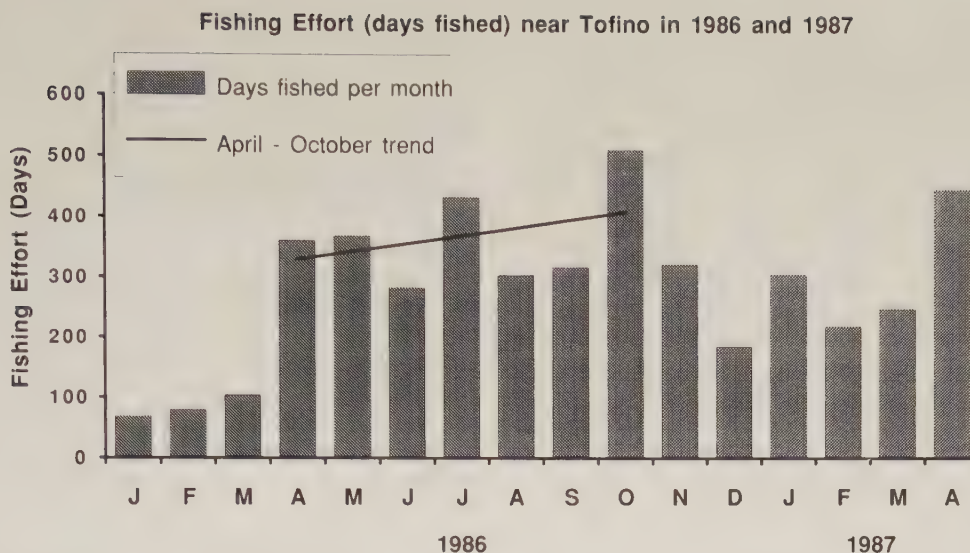


FIG. 1. Histogram of commercial fishing effort (days fished) on Dungeness crab for Canadian Department of Fisheries and Oceans Statistical Area 24 during 1986 and spring 1987. Statistical Area 24 includes, but is not limited to, the Tofino study site. The solid line indicates the linear trend in fishing effort for the period April until October 1986. The slope of this line is not significantly ($p > 0.05$) different from zero.

sented in Butler's and Hankin's comment indicated no significant linear trend in effort over the recovery period of April until October 1986 ($p > 0.05$, Fig. 1). The mean number of days fished from April until October 1986 was 369 d with a SD of 88 d. The corresponding coefficient of variation of about 25% is modest. We chose not to incorporate Statistical Area 24 effort data in our estimate of fishing mortality because those effort data do not directly correspond to our study site. Our Tofino study site includes only a portion of Statistical Area 24. We judged from preliminary estimates using those data that they did not improve the reliability of our estimate of fishing mortality. Butler and Hankin also refer to nonconstancy of effort in 1985, but such nonconstancy plays no role in any of the analyses we presented in Smith and Jamieson (1989b).

Interestingly, a more important limitation of our regression analysis in fig. 2 of Smith and Jamieson (1989b) is the expanding variance with time-at-large due to the small number of individuals recovered per 15-d interval after about 3–4 mo (see Gulland 1983). Consequently, those data points based on only a few recoveries can overly influence the regression line. There are better approaches to this problem and we applied one of the improved methodologies in Smith and Jamieson (1990).

Our calculation of an annual instantaneous total mortality rate (Z) of 9.2 expresses total mortality as an annual rate based on a simple extrapolation to a full year of our estimate of the rate of decline in recovery of tagged legal-sized males from fig. 2 of Smith and Jamieson (1989b). Since most of the moulting to legal size that occurred during 1986 was completed by the end of October (fig. 4B of Smith and Jamieson 1989b), and fishing effort from April 1986 until April 1987 displayed no dramatic linear trends (slope not significantly different from zero, $p > 0.05$), we considered $Z = 9.2$ a fair estimate of the total mortality experienced by the population of crabs which moulted to legal size during 1986. Fishing effort (days fished) from April 1986 until April 1987 averaged 332 d with a SD of 97 d (Fig. 1). The corresponding coefficient of variation is about 30%.

3. Confounding of natural mortality with moulting to legal size

Here, Butler and Hankin argue that the disappearance of sublegal-sized crabs as portrayed in fig. 1 of Smith and Jamieson (1989b) could have resulted not only from natural mortality, but also moulting into legal size or fishing-related handling mortality. We agree and made that same point in Smith and Jamieson (1989b). The degree to which fishing-related handling mortality affects our estimate of natural mortality from fig. 1 in Smith and Jamieson (1989b) is unknown. It is not uncommon for fishermen to handle 10–20 sublegal crabs per trap haul, so handling can be extensive. Having repeatedly recovered the same tagged crabs up to seven times also indicates that crabs spend a lot of time in and around traps.

Butler and Hankin argue that moulting probabilities must be near 1 for those sublegal-sized crabs we tagged (mainly between January and May) in the size range 140–155 mm CW. Consequently, those males would have been expected to moult within the next few months to legal size. They suggest that the decline in sublegal-sized crabs plotted in fig. 1 of Smith and Jamieson (1989b) can be caused by moulting to legal size and that we did not recover those tagged crabs. Here we disagree.

Our purpose in tagging sublegal-sized crabs in the spring was to monitor their moult to legal size. As time went by the pattern of recovery clearly indicated that smaller, sublegal-tagged crabs were more likely to be caught as legal-sized crabs than larger, sublegal-tagged crabs. As Table 2 in Smith and Jamieson (1989b) relates, tagged crabs 125–130 mm CW were caught as legal-sized crabs in much greater proportion to their abundance than crabs 150–155 mm CW. We closely monitored this fishery near Tofino and do not believe that we simply failed to recover tagged legal-sized males. Our belief to date is that the larger sublegal-sized males (about 145–155 mm CW) generally did not moult in 1986. We think they died. Our best guess as to why this occurred is that many of these males did not have the energy reserves or health to moult. We do not have a specific explanation as to why this requirement might not have been met.

Hankin et al. (1985) introduced the idea of senescence for female Dungeness crabs in conjunction with increased mortality and decreased moulting probabilities. We share their idea and believe we have observed the same process for males near Tofino. The decrepit visual appearance and lack of vitality of many hard-shelled, large sublegal-sized males seemed consistent with senescence and mortality prior to, or perhaps during, a moult to legal size. In contrast, recently moulted crabs 140–155 mm CW were more vigorous, looked healthier, and were more difficult to handle safely than crabs of the same size that had experienced a longer intermoult period. Our data have thus led us to think that a male 130–135 mm CW is more likely to survive to legal size than a male 150–155 mm CW. Curiously, Butler and Hankin and Hankin et al. (1985, 1989) report increasing mortality with increasing CW for female Dungeness crabs, but seem reluctant to accept the same argument for male Dungeness crabs.

4. Uncertain shell condition of tagged crabs

Male crabs that we tagged near Tofino in 1985–86 did vary in shell hardness. We assessed shell hardness subjectively, based on touch, for the approximately 33 000 crabs that we handled during the period of our study. Although we cannot explicitly determine from our data how shell hardness affects tagging-related mortality, we were careful not to tag and release crabs that had particularly soft shells. We emphasized the tagging of sublegal-sized, hard-shelled males, since our objective was to monitor their moult to legal size. We had an interest in assuring that the crabs we tagged appeared healthy and strong.

A particular concern we had was that the smaller sublegal-sized males we tagged would be more traumatized by the tagging operation than larger crabs because of their thinner and more flexible shell, even when they had not recently moulted. In fact, our data on shell hardness at release indicate that a greater proportion of smaller sublegal-sized males tended to have softer shells than larger sublegal-sized males. However, the higher proportional recovery rate of tagged legal-sized males that were in the smaller size-classes when tagged suggested to us that these sizes of crabs were tolerating the tagging operation at least as well as larger crabs.

Application of Hoenig's (1983) method

Butler's and Hankin's use of Hoenig's (1983) statistical methodology to relate maximum longevity of a species to estimates of natural mortality deserves some comment. Butler and Hankin use Hoenig's (1983) fig. 1 and associated regression analyses to support their argument that natural mortality for male Dungeness crabs near Tofino during our study should range from $M = 0.8$ – 1.2 . In making this inference, Butler and Hankin do not acknowledge that the figures presented by Hoenig (1983) simply portray empirical data which conform to a qualitative relationship between longevity and estimates of mortality. Making a statistical prediction of mortality from estimates of maximum longevity requires knowledge of the sample size from which maximum age was inferred. This information is absent from Hoenig's (1983) figures and the regression equation Butler and Hankin used.

We can use Hoenig's (1983) statistical theory to draw inferences and expectations regarding total mortality of legal-sized males during our study. Hoenig (1983) introduces

$$E[t_{\max}] \approx \frac{\ln(2n + 1)}{Z} + t_c$$

where $E[t_{\max}]$ is the expected age of the oldest individual within a sample of size n . The parameter Z is total mortality and t_c is the age at which individuals are fully selected by the fishing gear. If we set t_c to zero to represent the time when a male moults to legal size and assume that legal-sized males are approximately uniformly selected by traps (Smith and Jamieson 1989a), then $E[t_{\max}]$ will represent the life expectancy of the oldest legal-sized male sampled. Adding our revised estimate of $M = 2.5$ (Smith and Jamieson 1990) and our central estimate of $F = 6$ (Smith and Jamieson 1989b) gives $Z = 8.5$. During our study, we measured more than 2500 legal-sized males, thus yielding a maximum life expectancy for a legal-sized male of about 1 yr.

The largest males we sampled during our study ranged between 180 and 185 mm CW. Based on the growth analysis of Smith and Jamieson (1989c), males in this size range would be expected to be members of the instar with a mean CW of 185 mm (SD = 14 mm). This instar would be composed almost entirely of legal-sized males. However, numerous size frequency analyses on trap-caught males near Tofino (unpublished data) never resulted in the statistical detection of members of this instar. Statistically, crabs this size were more likely to be large members of the 156-mm instar. Only size frequency analyses of males trap-caught in the lightly exploited Holberg Inlet fishery (see Smith and Jamieson 1991) resulted in members of the 185-mm instar being detected. (The Holberg Inlet analyses assumed the instar descriptions determined for Tofino.) Our inference from such analyses was that the combination of natural mortality and exploitation of legal-sized males in the 156-mm instar (SD = 13 mm) is high enough to preclude virtually all of them from surviving the intermoult period between the 156- and 185-mm instar. If 1 yr is a reasonable expectation of the intermoult period for males near legal size, then our estimate of $Z = 8.5$ is consistent with the observed CW's of legal-sized males.

Concluding remarks

Butler and Hankin are welcome to present their ideas and best guesses regarding the natural and fishing mortality rates of male Dungeness crabs near Tofino, B.C., during 1985 and 1986. Readers should realize, however, that their estimate is based on beliefs developed from experience with Dungeness crab fisheries elsewhere and the imposition of general ideas about mortality upon a specific fishery at a specific time. Neither author participated in the study of Dungeness crab dynamics near Tofino during 1985–86, nor to the best of our knowledge has either author experience with this fishery.

In contrast, B.D.S. and others participating in this 2-yr study spent approximately 2 wk a month sampling and tagging crabs, recovering tagged crabs, and interviewing fishermen in an attempt to document some of the dynamics of this fishery. During this time (as mentioned in Smith and Jamieson 1989b), we witnessed the passage of an unusually strong cohort (probably the 1983 year-class) through this fishery. It is conceivable that our estimated rate of natural mortality during the period of our study is a result of density effects from unusually high crab abundance. Our estimated rate of fishing mortality can result from intense intraspecific competition arising from an unusually high crab abundance and rapid exploitation by a responsive local supply of fishermen predators.

Only further research will resolve whether the mortality results we obtained for this fishery in 1985–86 are typical for the Dungeness crab population near Tofino. We remain open-minded to new information from mark-recapture, catch-per-

unit-effort, and size frequency data, etc., that furthers our understanding of Dungeness crab mortality dynamics. For the moment, we stand by our estimate of $M = 2.3\text{--}2.8$ (Smith and Jamieson 1990) for sublegal-sized male Dungeness crabs near Tofino, but fully acknowledge that fishing-related handling mortality, density effects, etc., are likely to contribute something to this high value and perhaps cause it to be peculiar to this particular site during 1985–86. We have never claimed otherwise. It is scientifically interesting, however, that this same study (Smith and Jamieson 1990) provided estimates of female Dungeness annual natural mortality near Tofino of about 1.3 which is similar to estimates obtained by Hankin et al. (1985, 1989) for females of a similar size range in northern California — Barry D. Smith, *Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616 USA*, and Glen S. Jamieson, *Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada*. (JB461)

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ANNOUNCEMENTS/AVIS

Canadian Conference for Fisheries Research (CCFFR)

*Trent University
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Announcement of Conference and Call for Papers

This conference will be held in Peterborough, Ontario, January 3 and 4, 1993.

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A workshop is also planned on the following topic: Use of scientific information on fish for setting objectives towards fostering ecosystem integrity.

While papers on other themes may be submitted, authors are encouraged to adhere to the above themes as much as possible.

Deadline for abstracts is **August 30, 1992**. They should be typed (maximum 200 words, single spaced) and nature of presentation (oral/poster) indicated. A high quality of copy is required, suitable for photographic reproduction.

Abstracts should be addressed to Dr. Daniel Boisclair, Biological Sciences Department, University of Montreal, P.O. Box 6128, Station "A", Montreal, Que. H3C 3J7, Canada. Tel. (514) 343-6762.

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*Université Trent
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